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FEEDING HABITS OF COMMON SNOOK, *CENTROPOMUS UNDECIMALIS*, IN CHARLOTTE HARBOR, FLORIDA

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ABSTRACT We examined the feeding habits, ontogenetic and seasonal diet variations, and predator size–prey size relationships of common snook, *Centropomus undecimalis*, in Charlotte Harbor, Florida, through stomach contents analysis. A total of 694 stomachs were extracted from common snook (300–882 mm standard length [SL]) during a 24-month period (March 2000–February 2002); 432 stomachs contained prey items. At least 37 prey taxa were identified, including 19 that had not been previously reported. Fishes made up 71% of the prey by number and 90% by weight. Three prey items made up almost 50% of the diet numerically—*Lagodon rhomboides*, *Anchoa* spp., and *Farfantepenaeus duorarum*. Seven species made up more than 60% of the diet by weight—*L. rhomboides*, *Cynoscion nebulosus*, *Mugil gyrans, Bairdiella chrysoura*, *Synodus foetens*, *Orthopristis chrysoptera*, and *Mugil cephalus*. An ontogenetic shift in prey preference was identified in adult common snook at around 550 mm SL. Smaller individuals (300–549 mm SL) ate more *F. duorarum*, palaemonid shrimp, cyprinodontids, and *Eucinostomus* spp. than did larger individuals (550–882 mm SL), which ate more *S. foetens*, ariids, and sciaenids. Significant, positive relationships between predator size and prey size were observed between common snook and *L. rhomboides*, *O. chrysoptera*, portunid crabs, and all fish prey combined. Prey size selection contributed to some seasonal differences in their diet. For example, in winter when *L. rhomboides* are abundant in the estuary and small in size (mean = 23 mm SL), common snook ate few individuals, but they consumed many during summer when larger *L. rhomboides* (mean = 51 mm SL) were available. In summary, common snook are opportunistic predators that feed on a wide variety of prey and exploit specific-sized prey that are abundant in their environment.

INTRODUCTION

Common snook, *Centropomus undecimalis*, inhabit tropical and subtropical estuarine systems of the western Atlantic from about 34°N to about 25°S latitude (Rivas 1986). In Florida, they occur principally from Cape Canaveral on the Atlantic coast southward around the peninsula to Cedar Key on the Gulf of Mexico coast (Taylor et al. 2000). The Common snook is a euryhaline, diadromous species that is found in a wide variety of habitats but typically associates with mangrove shorelines (Marshall 1958). They are protandric hermaphrodites that attain ages of 21 years, grow to more than 1000 mm fork length (FL) (Taylor et al. 2000), and have an important ecological role as one of the top predators in the estuary.
Common snook are popular gamefish that support a large recreational fishery throughout much of coastal south and central Florida (Muller and Taylor 2002). Concerns of overfishing and habitat loss have stimulated considerable research on this species over the past 50 years. Much of the research has focused on understanding its life history in order to properly manage the stocks (Peters et al. 1998, Taylor et al. 1998, 2000).

One aspect of the common snook life history that requires further exploration is the feeding habits of adults (50% of common snook mature at 330 mm SL; Peters et al., 1998). Gilmore et al. (1983) and McMichael et al. (1989) collected principally juveniles from the Indian River Lagoon and Tampa Bay respectively, for stomach-content analysis. In contrast, Marshall (1958) and Fore and Schmidt (1973) examined the diet of adult common snook collected from the Ten Thousand Islands and from the Atlantic coast of Florida; however, these 2 studies were limited in sample size and duration. Fore and Schmidt (1973) analyzed ontogenetic shifts, but prey were grouped into 3 categories (fish, shrimp, and crabs), so the importance of individual species or taxa was not reported.

The previous diet studies on adult common snook provide a valuable foundation of information; however, a long-term, system-wide detailed analysis in an estuary would enable spatial and seasonal diet trends to be examined, as well as ontogenetic shifts in prey preference. A large sample size would also provide adequate prey length data for examining predator size-prey size relationships. The Fish and Wildlife Research Institute's Fisheries-Independent Monitoring (FIM) program collects long-term, comprehensive baseline data on relative abundances of fishes and selected macroinvertebrates in most of Florida's estuaries. Collections from this program provided year-round, estuary-wide random samples of common snook as well as their potential prey. In this paper, we describe the feeding habits of common snook from Charlotte Harbor, a relatively pristine estuary (~ 80% of shoreline protected from development; R. Repenning, Florida Department of Environmental Protection, pers. comm.) located along the Gulf of Mexico in southwestern

Florida. We assessed 1) ontogenetic, spatial, and seasonal variation in the prey composition, 2) predator size–prey size relationships, and 3) size-selective feeding patterns.

MATERIALS AND METHODS

Collections

We examined the stomachs of 694 common snook (300–882 mm standard length [SL]) collected from the estuarine waters of Charlotte Harbor during a 24-month period between March 2000 and February 2002 (Figure 1). Common snook were collected with a 183-m center-bag seine (38-mm stretched mesh) during the daylight hours of 0900–1600 by the FIM program. A standardized random sampling protocol was followed for all collections, and a total of 408 samples (17/mo) were collected along the shoreline in depths of 2.5-m or less (see Kupschus and Tremain (2001) for a detailed description of the survey design, deployment techniques, and sample processing). Samples came principally from mangrove and seagrass habitats, which are predominant within the Charlotte Harbor estuary (Poulakis et al. 2003). Common snook were selected for stomach-content analysis from 44% of the sampling sites, and a mean of 3 individuals were sampled from each site (range = 1–11 individuals). Common snook were iced immediately after capture in the field, and transported to the laboratory, where SL was measured to the nearest millimeter (mm) and stomachs were removed, sealed in bags, and frozen (Meyers and Franks 1996, Scharf and Schlicht 2000). Stomachs were thawed within one month of collection and the contents of each were sorted and identified to the lowest possible taxon. Pieces of prey items were counted as one, unless countable parts such as otoliths or eye lenses were found. A reference collection of otoliths from potential prey within the estuary was established and was used to identify badly decomposed fish prey items. All whole prey were measured to the nearest mm (SL for fish, post-orbital head length [POHL] for shrimp, and carapace width [CW] for crabs) and weighed to the nearest tenth of a gram (g).

To compare the diet of common snook with potential prey in the estuary, we examined availability, size, and seasonality of potential prey from 21.3-m and 183-m center-bag seine collections from shoreline areas throughout the estuary (183-m seine collections are described above). Each month 21.3-m seines (3-mm stretched mesh) were pulled along shorelines (depth < 1.5 m) at 12 random sites throughout the estuary. The collected fish were measured for SL, and shrimp were measured for POHL (see Poulakis et al. 2003) for a detailed description of sample processing). Stomach contents were evaluated as: 1) percent numerical abundance (N) = the number of individuals of each food type as a percentage of the total number of identifiable prey items, 2) percent weight (W) = wet weight (g) as a percentage of the total wet weight of all prey items, and 3) percent frequency of occurrence (F) = the percentage of stomachs containing prey in which a particular prey taxon occurred.

Data Analysis

Nonparametric multivariate techniques were used to analyze ontogenetic, spatial, and seasonal changes in the diet of common snook. To identify length-related differences in feeding, we used a hierarchical agglomerative cluster analysis (CLUSTER) based on square-root transformed Bray-Curtis similarity coefficients from prey-numeric data, which incorporated a group-average linking method (Clarke 1993, Clarke and Warwick 2001). We grouped common snook that ranged in size from 300 to 599 mm into 25-mm SL size intervals. Common snook ≥600 mm SL were not as abundant in our collections as those <600 mm, so larger individuals were grouped into 100-mm SL intervals to attain length-class sample sizes similar to those of smaller common snook. Only common snook that contained identifiable prey to at least the family level were used. Within a particular family or genus in which all prey items could not be identified to species, prey items were assigned to the lowest taxon (e.g., *Eucinostomus gula*, *Eucinostomus* spp. = *Eucinostomus* spp.; *Ariopsis felis*, UID Ariidae = UID Ariidae). Based on this cluster analysis, stomach contents of length-classes < 550 mm SL showed a level of similarity of > 55%, and this size class for this study is termed "small" (n = 293). Fish that were ≥ 550 mm SL are termed "large" (n = 51). To minimize the effects of length-related dietary shifts, only small common snook were used for the size-selective feeding, spatial, and seasonal analyses.

Predator size-prey size relationships were examined by plotting common snook length against prey length. Spearman rank correlations were used to determine any significant relationship between common snook length and the length of their prey.

Size-selective feeding patterns of small common snook were examined for the 3 most abundant prey species. Length frequencies and abundances of these species were determined from 21.3-m seine collections. Combined catches from the 21.3-m and 183-m seines were used only for *Lagodon rhomboides* (pinfish), which had a broad size range (15–225 mm SL) and were not adequately sampled with only the 21.3-m seine. All abundance data for seines are reported as number·100 m^{-2}. Length frequencies of prey from common snook stomachs were compared to length frequencies from seine collections in the estuary

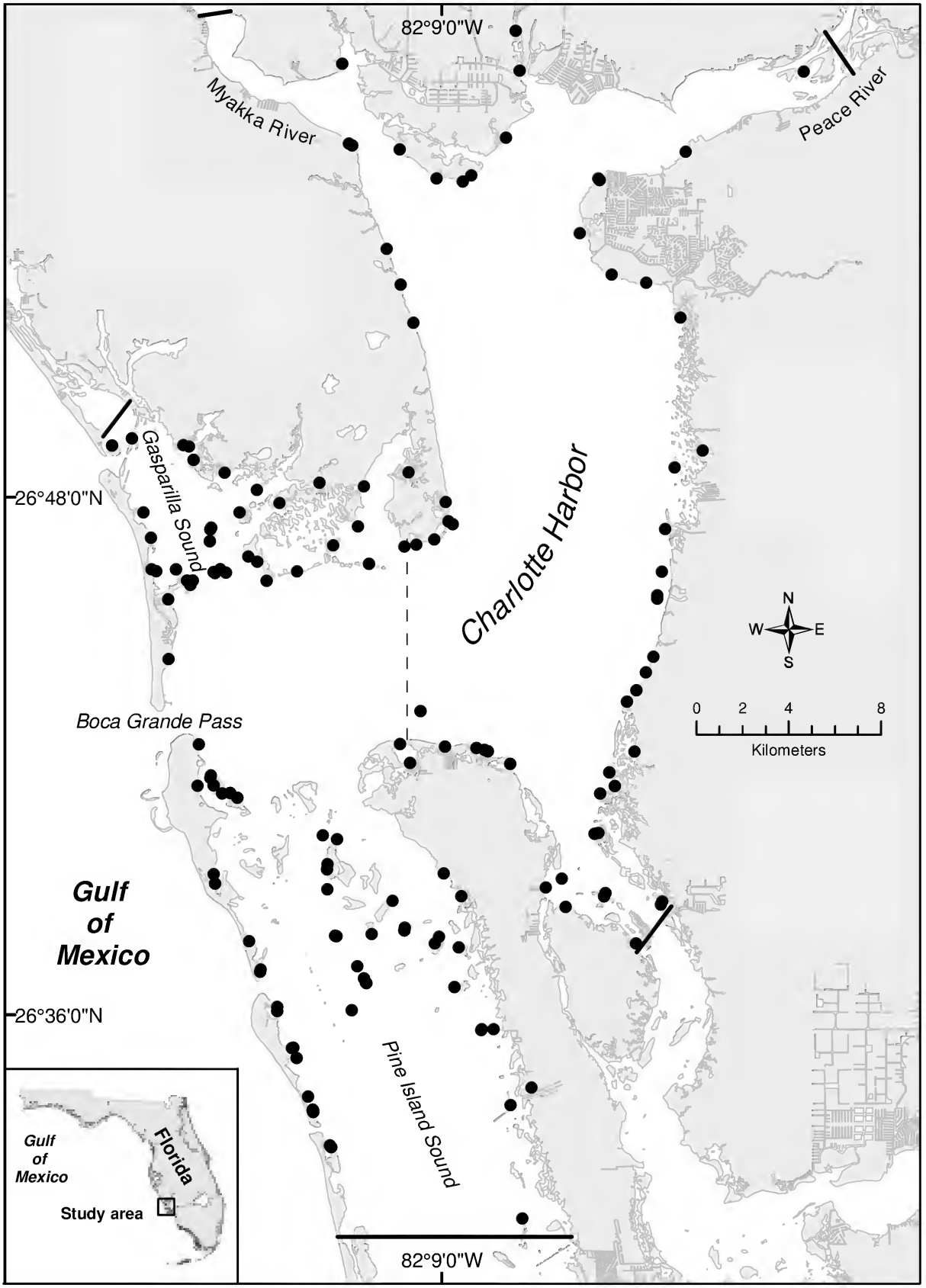

Figure 1. Map of Charlotte Harbor, Florida, showing the collection locations of common snook, *Centropomus undecimalis*, whose stomachs contained prey. The dark lines denote the Fisheries-Independent Monitoring program sampling universe boundaries, and the dotted vertical line denotes the separation between the "east area" and the "west area".

(Kolmogorov-Smirnov [KS] two-sample test, Sokal and Rohlf 1981).

Differences in the diet of small common snook were compared between the eastern half (i.e., "east area") and the western half (i.e., "west area") of the estuary (Figure 1). The east area is more influenced by freshwater inflow from major rivers, whereas the west area is more influenced by the Gulf of Mexico through 4 gulf passes (Rubec et al. 1999). To compare the prey composition of common snook from the 2 areas, prey-numeric data were square-root transformed, and an analysis of similarity (ANOSIM) permutation test was used and the R-value was used to determine significance (Clarke 1993, Clarke and Warwick 2001). To minimize confounding seasonal effects (unequal seasonal representation of the 2 areas) on the spatial analysis, some stomach samples were randomly eliminated from the west area. As a result, each area had 17 winter, 33 spring, 29 summer, and 37 fall samples.

To determine if there was any seasonal variation in the diet of small common snook, samples were grouped by season: winter (December–February; $n = 36$), spring (March–May; $n = 78$), summer (June–August; $n = 104$), and fall (September–November; $n = 75$) (Cortes et al. 1996, Crabtree et al. 1998). The prey community data (numeric) from each season were square-root transformed, and 6 pairwise comparisons were made among seasons using ANOSIM. Also, seasonal mean prey size and mean abundance determined from stomach-content and seine data were compared to illustrate how the size and availability of prey items are related to their seasonal consumption by common snook.

RESULTS

Stomachs of 432 common snook ranging from 300 to 822 mm SL contained prey, and those of 262 common snook were empty (Figure 2). Fishes and crustaceans made up virtually all of the prey by number (97%) and weight (98%) (Table 1). At least 37 different prey taxa were identified with 3 prey taxa comprising almost 50% of the diet numerically—*L. rhomboides* (pinfish; 20%), *Anchoa* spp. (anchovy; 16%), and *Farfantepenaeus duorarum* (pink shrimp; 13%). *Anchoa* spp. were eaten by common snook in high numbers but were consumed less frequently ($F = 7\%$) than *L. rhomboides* (32%) and *F. duorarum* (20%). Seven species made up more than 60% of the diet by weight—*L. rhomboides* (22%), *Cynoscion nebulosus* (spotted seatrout; 9%), *Mugil gyrans* (whirligig mullet; 8%), *Bairdiella chrysoura* (silver perch; 7%), *Synodus foetens* (inshore lizardfish; 6%), *Orthopristis chrysoptera* (pigfish; 6%), and *Mugil cephalus* (striped mullet; 6%).

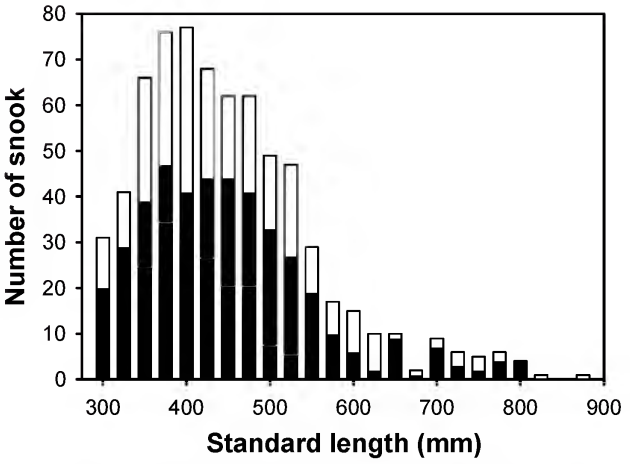

Figure 2. Length-frequency distribution of 694 common snook, *Centropomus undecimalis*, collected in Charlotte Harbor. Common snook with prey found in the stomachs are represented by black bars ($n = 432$), and common snook with empty stomachs are represented by white bars ($n = 262$).

Cynoscion nebulosus, *M. gyrans*, *S. foetens*, and *M. cephalus* were generally large prey items that were neither abundant in the diet nor frequent in occurrence ($N < 0.4\%$; $F < 0.6\%$).

Fish were the principal prey both numerically and by weight for all sizes of common snook examined (Figure 3). Fish made up almost 100% of the diet by weight of common snook ≥ 575 mm SL. Shrimp were more important in the diet of common snook 300–499 mm SL, both numerically and by weight, than in that of common snook ≥ 500 mm SL. Crabs were principally consumed by common snook 425–724 mm SL (N range 5–20%) but made up only < 0.1–7% of the diet by weight for common snook ≥ 575 m SL.

Small common snook (< 550 mm SL) had prey compositions with a high level of similarity (> 55%) and were grouped together in the cluster analysis (Figure 4). Prey compositions among large common snook (≥ 550 mm SL) length groups varied and were 5–25% different from those of small common snook. Small common snook ate more shrimp, small crabs, and small forage fish than did large common snook (Table 2). Palaemonid shrimp (grass shrimp), grapsid crabs (marsh crabs), cyprinodontids (killifishes), atherinopsids (silversides), and *Eucinostomus* spp. (mojarras) were found in the stomachs of only small common snook. Large common snook consumed more *S. foetens*, ariids (sea catfishes), and sciaenids (drums) than did small common snook. Both size-groups fed on clupeids (herrings), *O. chrysoptera*, *L. rhomboides*, and *B. chrysoura*, and stomach contents of both groups had a high frequency of occurrence of seagrasses ($F > 25\%$) (*Thalassia testudinum* [turtle grass], *Halodule wrightii*

TABLE 1

Prey items (n = 1133; total weight = 4913 g) found in stomachs of common snook (n = 432) collected in Charlotte Harbor, Florida. N = percent numerical abundance, W = percent weight, F = percent frequency of occurrence, UID = unidentified prey.

Prey category	N	W	F	Prey category	N	W	F
Stomatopoda	0.3	0.2	0.2	Fundulidae			
Squilla empusa	0.3	0.2	0.2	*Fundulus similis*	0.2	< 0.1	0.5
Decapoda	25.9	7.5	34.7	*Fundulus grandis*	0.3	0.5	0.5
Penaeidae				*Fundulus* spp.	0.4	0.2	0.7
Farfantepenaeus duorarum	12.6	3.1	20.1	Lucania parva	0.2	< 0.1	0.5
Palaemonidae				Poeciliidae			
UID Palaemonidae	4.3	< 0.1	5.8	*Poecilia latipinna*	0.3	0.1	0.7
Alpheidae				Cyprinodontidae			
UID Alpheidae	0.4	< 0.1	0.9	*Cyprinodon variegatus*	1.2	0.3	1.6
UID shrimp	1.2	< 0.1	2.1	*Floridichthys carpio*	0.7	0.3	0.9
Majidae				Opistognathidae			
UID Majidae	< 0.1	0.2	0.2	*Opistognathus robinsi*	< 0.1	0.2	0.2
Portunidae				Gerreidae			
UID Portunidae	0.4	< 0.1	0.9	*Eucinostomus gula*	0.4	0.3	0.9
Callinectes sapidus	0.9	2.2	2.1	*Eucinostomus* spp.	2.6	0.9	4.6
Portunus spp.	0.9	0.6	2.1	*Diapterus*/*Eugerres* spp.	< 0.1	0.2	0.2
Xanthidae				Haemulidae			
UID Xanthidae	0.2	< 0.1	0.5	*Orthopristis chrysoptera*	1.5	5.8	3.9
Grapsidae				Sparidae			
UID Grapsidae	0.6	< 0.1	0.5	*Lagodon rhomboides*	19.6	22.2	31.5
Armases mierii	0.8	0.3	0.2	Sciaenidae			
Ocypodidae				*Cynoscion nebulosus*	0.2	9.2	0.5
Uca spp.	1.4	0.4	1.9	*Cynoscion* spp.	0.4	0.5	0.9
Uca thayeri	< 0.1	< 0.1	0.2	*Bairdiella chrysoura*	2.8	6.6	6.5
UID crabs	2.1	0.2	3.7	*Leiostomus xanthurus*	< 0.1	2.3	0.2
Teleostei	71	90	84.3	Sciaenops ocellatus	< 0.1	4.7	0.2
Elopidae				Gobiidae			
Elops saurus	< 0.1	1.5	0.2	*Microgobius gulosus*	1.6	< 0.1	1.2
Engraulidae				UID fish	16.8	2.3	31.3
Anchoa spp.	15.7	1.5	7.4	Incidentals	2.8	2.3	40.6
Clupeidae				Plant Material			
UID Clupeidae	2.7	3.3	3.9	Algae	-	0.3	9.3
Harengula jaguana	0.5	2.8	1.2	Leaf Litter	-	0.1	3.5
Brevoortia spp.	< 0.1	3.4	0.2	*Thalassia testudinum*	-	1.3	21.9
Opisthonema oglinum	< 0.1	0.1	0.2	*Halodule wrightii*	-	0.1	16.7
Ariidae				*Syringodium filiforme*	-	0.3	8.3
UID Ariidae	0.4	0.3	0.7	Gastropoda	1.6	< 0.1	2.9
Ariopsis felis	0.3	0.7	0.5	Bivalvia	0.6	< 0.1	1.6
Synodontidae				Isopoda	0.4	< 0.1	1.2
Synodus foetens	0.3	6.1	0.7	Miscellaneous material			
Mugilidae				Fishing hook	0.2	< 0.1	0.5
Mugil cephalus	< 0.1	5.5	0.2				
Mugil gyrans	0.2	7.8	0.5				
Mugil spp.	0.6	< 0.1	0.5				
Atherinopsidae							
UID Atherinopsidae	*0.5*	*< 0.1*	*1.2*				

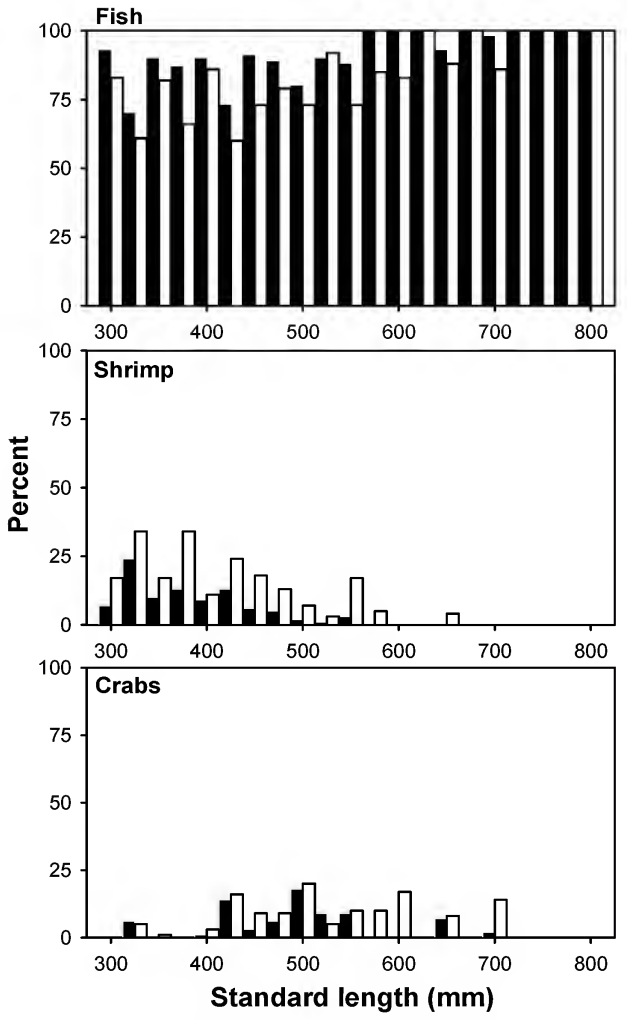

Figure 3. Percentages of weight (black) and number (white) of prey groups for each 25-mm size-class of common snook, *Centropomus undecimalis*, collected in Charlotte Harbor.

[shoal grass], or *Syringodium filiforme* [manatee grass]). Seagrasses were most consistently ingested (51–65%) with *L. rhomboides*, *O. chrysoptera*, and *Cynoscion* spp. (seatrout).

Common snook ranging from 300 to 822 mm SL ate fishes ranging from 12 to 307 mm SL, shrimp 4–36 mm POHL, and crabs 9–76 mm CW. A significant predator size-prey size relationship was observed between common snook and fish prey (Spearman Rank Correlation, R=0.41, $P < 0.0001$; Figure 5A). Common snook ate fish prey that averaged 14% of their own body length. The smallest fish prey consumed in relation to predator size was a 12-mm *Eucinostomus* spp. consumed by a 382-mm common snook (3% body length), and the largest was a 214-mm *M. gyrans* consumed by a 472-mm common snook (45% body length). Mean SL of fish prey for common snook 300–449 mm was between 45 and 47 mm and increased to 70 mm for common snook 450–549 mm (Figure 5B). Mean fish prey SL increased substantially to 110–179 mm in common snook 550–749 mm but dropped slightly to 140–164 mm for common snook 750–822 mm. Prey that were numerous and grew to large sizes, such as *L. rhomboides*, *O. chrysoptera*, and portunid crabs (swimming crabs), had a significant predator size-prey size relationship ($P < 0.03$; Figure 6). Small prey, such as *Eucinostomus* spp. and *F. duorarum*, were generally consumed by common snook < 500 mm and did not show a significant predator size–prey size relationship.

When comparing the sizes of prey eaten by small common snook to the sizes of the same prey species collected in the estuary, we found a significantly larger size distribution of *L. rhomboides* (45–75 mm SL) and *Anchoa* spp. (35–55 mm SL) in the stomachs of common snook than was collected in the estuary (KS test, $P < 0.0001$; Figure 7). There was no significant difference in the size distributions of *F. duorarum* collected in the estuary and those eaten by common snook (KS test, $P > 0.3$).

No significant difference was found between the diet of small common snook collected from the east and the west areas of the estuary (ANOSIM, R = 0.01; $P = 0.039$). Therefore, the diets of small common snook ($n = 293$) throughout the estuary were used for the seasonal diet comparisons.

Seasonal variation in the diet of small common snook was most evident between summer and winter (ANOSIM, R = 0.2; $P = 0.001$); all other seasonal pairwise tests had an R value of < 0.1. Common snook ate more than 10 times more *L. rhomboides* in summer (1.1 fish·stomach^{-1}) than in winter (0.1 fish·stomach^{-1}) (Figure 8). Young-of-the-year *L. rhomboides* (mean SL = 23 mm) recruited to the estuary during winter and were abundant (234 fish·100 m^{-2}). By summer, *L. rhomboides* grew to a mean size of 51-mm SL, and their abundance in the estuary dropped to 69 fish·100 m^{-2}. Common snook preyed upon *F. duorarum* consistently each season (0.33–0.64 shrimp·stomach^{-1}), with the highest rate of consumption occurring during winter (Figure 9). The mean size of *F. duorarum* collected in the estuary varied only slightly among the different seasons (12–15 mm POHL) but abundance was variable (5–44 shrimp·100 m^{-2}).

DISCUSSION

Common snook collected in Charlotte Harbor had a higher percentage of stomachs that contained prey (62%) compared to other studies. Marshall (1958) and Fore and Schmidt (1973) studied the diet of common snook (224–1020 mm FL) from the Ten Thousand Islands in

Table 2

Prey items found in stomachs of small (< 550 mm) and large (≥ 550 mm) common snook. Numbers in bold indicate taxa proportionally more important (both *N* and *W* varied by more than 50% between diets) in the diet of either small or large common snook. Only common snook with prey items identified to at least the family level were used (*n* = 344; UID = unidentified prey). *N* = percent numerical abundance, *W* = percent weight, *F* = percent frequency of occurrence.

	< 550 mm SL (*n* = 293)			≥ 550 mm SL (*n* = 51)		
Prey category	***N***	***W***	***F***	***N***	***W***	***F***
Decapoda						
Penaeidae						
Farfantepenaeus duorarum	**17.4**	**6.8**	**27.6**	7.8	0.4	11.8
UID Palaemonidae	**6.3**	**0.2**	**8.5**	0.0	0.0	0.0
UID Alpheidae	**0.5**	**0.2**	**1.4**	0.0	0.0	0.0
UID Grapsidae	**2.0**	**1.0**	**1.0**	0.0	0.0	0.0
Teleostei						
UID Clupeidae	4.3	11.6	4.4	5.6	7.4	9.8
Ariidae						
UID Ariidae	0.3	< 0.01	1.0	**6.7**	**1.4**	**11.8**
Synodontidae						
Synodus foetens	0.1	0.1	0.3	**2.2**	**11.9**	**3.9**
Atherinopsidae						
UID Atherinopsidae	**0.8**	**0.1**	**1.7**	0.0	0.0	0.0
Fundulidae						
Fundulus spp.	**1.1**	**1.8**	**1.0**	0.0	0.0	0.0
Cyprinodontidae						
Cyprinodon variegatus	**1.8**	**0.8**	**2.4**	0.0	0.0	0.0
Floridichthys carpio	**1.0**	**0.7**	**1.4**	0.0	0.0	0.0
Gerreidae						
Eucinostomus spp.	**4.3**	**2.9**	**6.8**	0.0	0.0	0.0
Haemulidae						
Orthopristis chysoptera	1.3	5.5	3.4	7.8	6.7	13.7
Sparidae						
Lagodon rhomboides	25.7	33.2	39.2	23.3	15.6	41.1
Sciaenidae						
Cynoscion spp.	0.5	1.2	0.7	**2.2**	**17.9**	**3.9**
Bairdiella chrysoura	3.2	11.0	7.2	7.8	3.6	13.7
Leiostomus xanthurus	0.0	0.0	0.0	**1.1**	**4.5**	**2.0**
Sciaenops ocellatus	0.0	0.0	0.0	**1.1**	**9.2**	**2.0**
Incidentals						
Plant Material						
Seagrasses	–	2.6	25.7	–	0.7	35.3

southwest Florida and reported that 48% and 46% of the stomachs of common snook had prey, respectively. An even greater difference is noted when we compare the percentage of common snook stomachs containing prey during summer in Charlotte Harbor (75%) with the percentages from Fore and Schmidt, who collected only during summer. Both of the previous studies used hook-and-line gear for most of the sample collections. This gear has the advantage of sampling habitats that cannot be sampled with a net; however, it selects fish that are actively feeding, which may possibly increase the number of fish collected with empty stomachs. Regurgitation of prey items caused by stress during capture is also a factor that may contribute to a higher occurrence of fish with empty stomachs. On

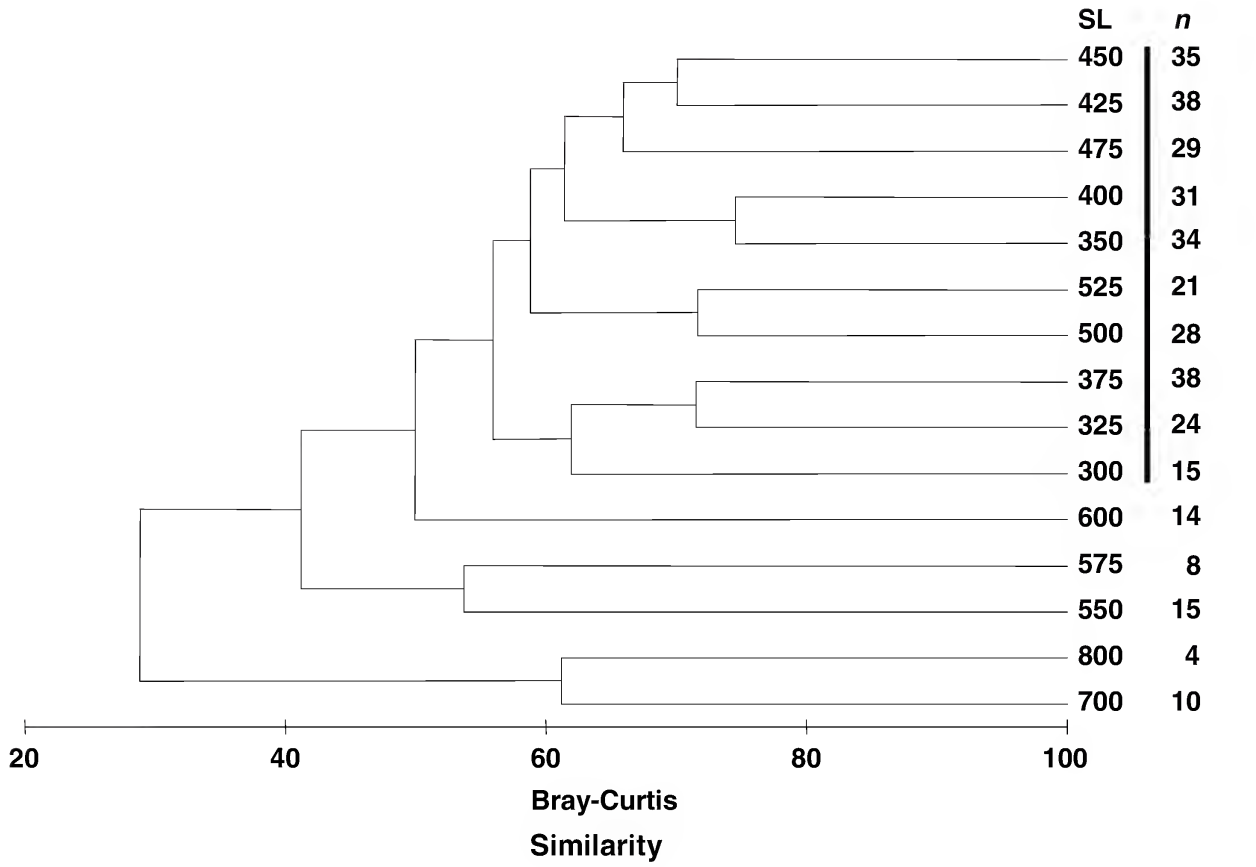

Figure 4. Cluster dendogram showing the percent similarities of prey composition in the different size-classes of common snook, *Centropomus undecimalis*. Common snook < 600 mm were grouped into 25-mm SL intervals and common snook ≥ 600 mm into 100-mm SL intervals. SL = lowest standard length of the length interval; *n* = number of common snook in each size-class. The dark vertical line denotes size-classes of common snook that have a > 55% similarity in diet.

only a few occasions did we observe regurgitated material within our nets, although small prey or pieces of prey could have gone through the mesh and would not have been detected. The use of a large bag seine, which allowed common snook to swim and move freely during retrieval, may have minimized capture stress and the likelihood of regurgitation.

The composition of fish (71%), shrimp (19%), and crabs (7%) in the diet of common snook in Charlotte Harbor was similar to that reported by Marshall (1958) (50% fish, 38% shrimp, 6% crabs), but differed with Fore and Schmidt (1973) (48% crabs, 26% shrimp, and 25% fish). The high percentage of crabs found by Fore and Schmidt may be partially attributed to their collections occurring exclusively in summer in the passes and cuts leading to the Gulf of Mexico during early-morning and late-evening, and at night under artificial lights. The most abundant prey found in their study was *Portunus gibbesii* (iridescent swimming crab; $N = 24\%$), which are found in large numbers during summer as they migrate through the passes and cuts to the open gulf to spawn (Rouse 1970, Dudley and Judy 1971). Our collections were made within the estuary during the daytime only, generally in areas with slower currents, and *Portunus* spp. were not a major component of the diet ($N < 1\%$). More in-depth trophic studies are needed to determine how estuarine location, habitat types within an estuary, diel periodicity, and lunar phase (related to tidal influence and light intensity at night) affect the diet of common snook.

A wide variety of prey was collected from the stomachs of common snook from Charlotte Harbor, suggesting that common snook have diverse feeding habits. Thirty-seven taxa were recorded, 19 of which had not yet been reported as prey (Marshall 1958, Fore and Schmidt 1973, Gilmore et al. 1983). Common snook fed on taxa that are pelagic, such as *Anchoa* spp. and clupeids (Jones et al. 1978) but also fed on taxa that are demersal, such as xanthid crabs (mud crabs), ariids, and *S. foetens* (Robins and

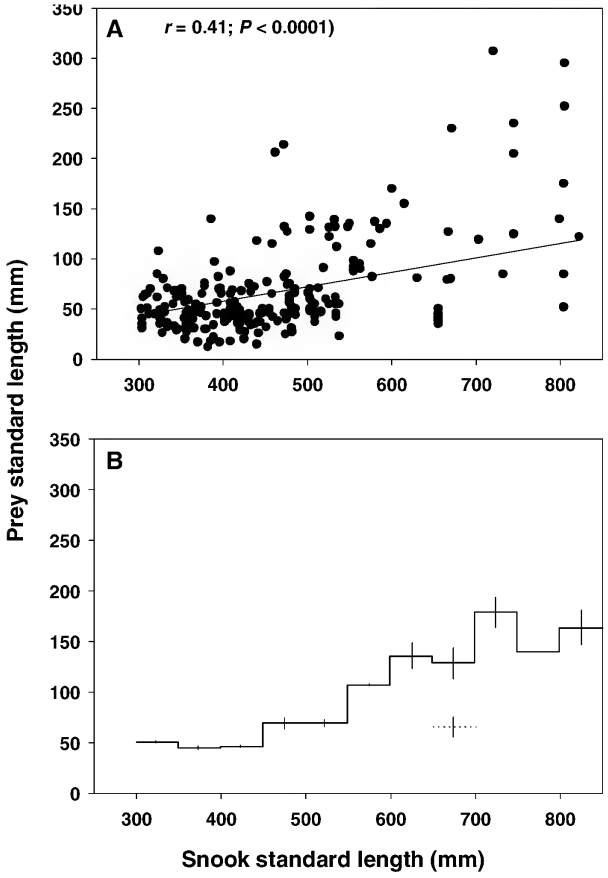

Figure 5. (A) Scatter diagram showing the relationship of prey size to the size of common snook, *Centropomus undecimalis*, for all teleost prey combined. Spearman rank correlation coefficient = *r*, and probability = *P*. (B) Horizontal line plot showing the mean prey size for each 50-mm size-class of common snook. Vertical lines represent ± standard error. The dotted horizontal line at size-class 675–699 mm SL includes one additional common snook that consumed 10 small *Anchoa* spp.

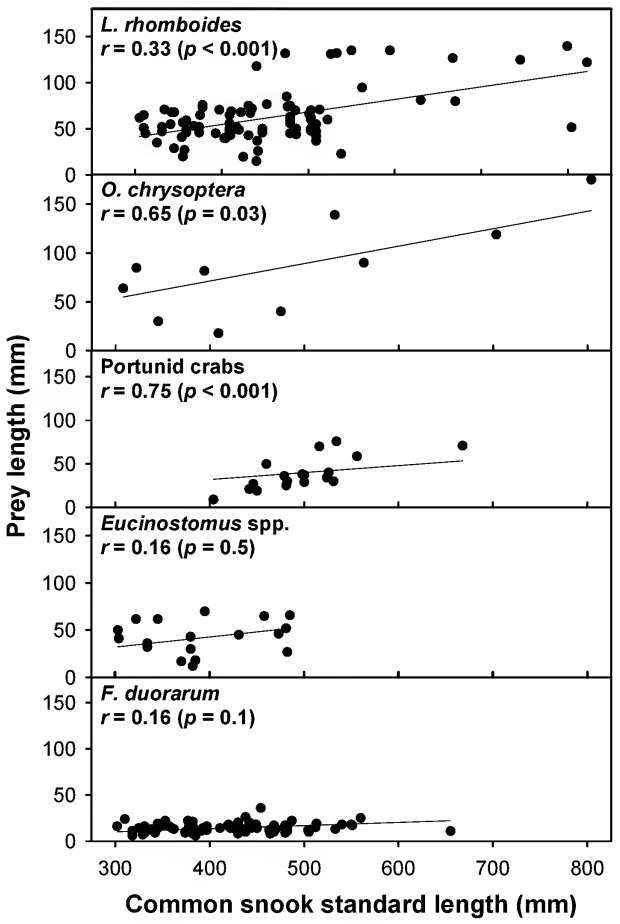

Figure 6. Scatter diagram showing the relationship between prey size and size of common snook, *Centropomus undecimalis*, for 5 important prey taxa. Spearman rank correlation coefficient = *r*, and probability = *P*.

Ray 1986, Pattillo 1997). They also fed on 5 taxa that are burrowers—*Squilla empusa* (mantis shrimp), alpheids (snapping shrimp), *Uca* spp. (fiddler crabs), *O. robinsi* (*spotfin jawfish*), and *Microgobius gulosus* (clown goby). Other taxa that common snook preyed on are both pelagic and demersal, such as *F. duorarum*, *Callinectes sapidus* (blue crab), and *Portunus* spp. Evidence suggests that common snook fed among the extensive intertidal prop roots and low branches of *Rhizophora mangle* (red mangrove) and *Avicennia germinans* (black mangrove), which dominate the shorelines of Charlotte Harbor. Prey items such as *Floridichthys carpio* (goldspotted killifish), *Poecilia latipinna* (sailfin molly), atherinopsids, and *Uca* spp. are highly associated with mangrove habitats (Thayer et al. 1987, Sheridan 1992, Poulakis et al. 2003). Common snook also appear to have fed in seagrass beds because seagrasses were present in the stomach along with prey items 37% of the time. Common snook ingest prey in a manner similar to other centropomids, such as *Lates calcarifer* (barramundi) (Hamblyn 1966, Davis 1985), which have no cutting or macerating teeth—the prey is drawn into the mouth by a powerful sucking action affected by the expansion of the buccal cavity and then swallowed whole. This mechanism can cause vegetation (i.e., seagrass, algae, leaf litter), gastropods, or shell material to be ingested along with the intended prey item. Taxa that prefer seagrass habitats, such as *L. rhomboides*, *O. chrysoptera*, and *Cynoscion* spp. (Nelson 1998, Nelson and Leffler 2001, Poulakis et al. 2003), were most often found in conjunction with seagrasses in the stomachs of common snook in Charlotte Harbor. Other species that common snook consumed are also associated with seagrass habitats during a portion of their life cycle (e.g., *F. duorarum*, *C. sapidus*, *B. chrysoura*) (Sheridan 1992, Poulakis et al. 2003). Common snook also appear to have fed over unvegetated

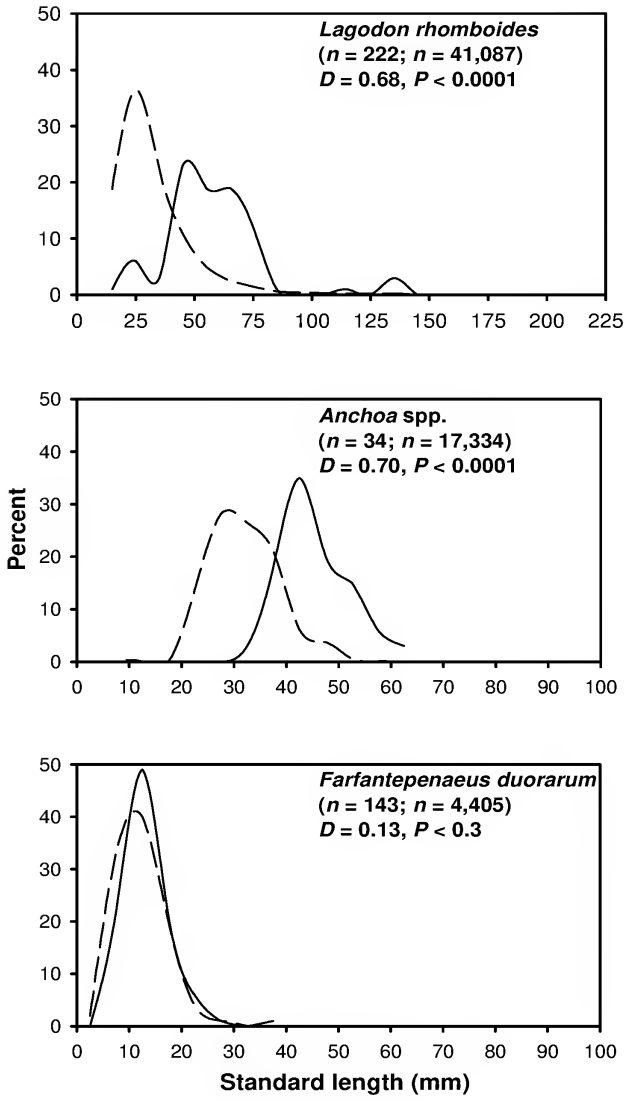

Figure 7. Length-frequency distributions of the top 3 numerically abundant prey taxa found in the stomachs of common snook, *Centropomus undecimalis*. The solid line represents the individuals consumed by common snook, and the first *n* value is the total number of individuals consumed. The dashed line represents the individuals collected in the estuary with the 21.3-m and 183-m shoreline seines, and the second *n* value is the total number of individuals collected from the estuary. The Kolmogorov-Smirnov (KS) two-sample test was used to compare length frequencies of prey collected in the estuary with prey consumed by common snook; *D* = maximum unsigned difference; *P* = probability.

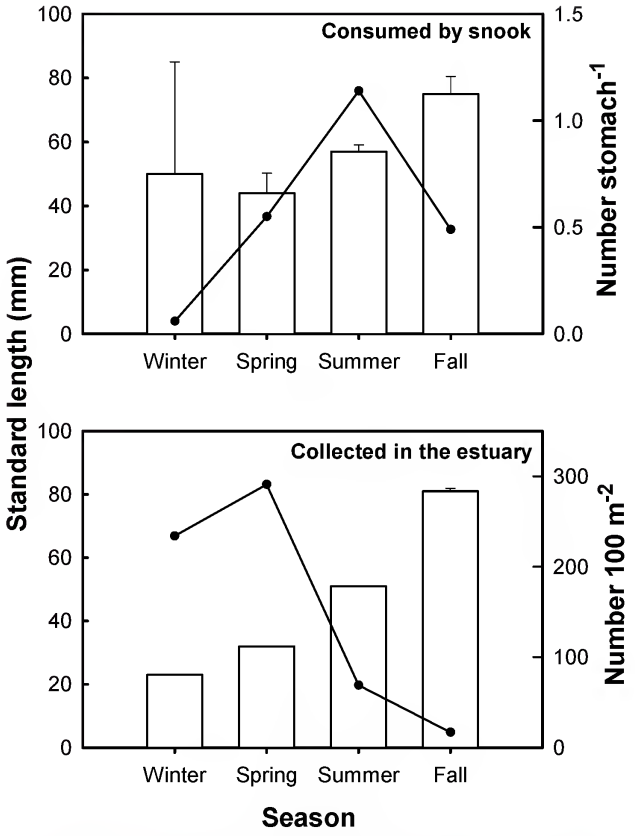

Figure 8. Plot of mean (± standard error) seasonal length (white bars) and abundance (points) for *Lagodon rhomboides* consumed by small common snook (< 550 mm SL), *Centropomus undecimalis*, and collected in the estuary with 21.3-m and 183-m shoreline seines. Some SE are too small to be seen.

bottom, as all ariids and *S. foetens* that were found in stomachs contained no fragments of seagrass, and these taxa are known to prefer open sand or mud bottoms (Springer and Woodburn 1960, Pattillo 1997). In summary, common snook in Charlotte Harbor appear to have fed on prey throughout the water column and in various habitats.

In Charlotte Harbor, the most abundant prey in the diet of common snook was *L. rhomboides* (19.6%), which may be attributed to the frequent occurrence of seagrasses along the shoreline. The shallow bottom of this estuary is dominated by seagrasses (262 km^2; Sargent et al. 1995) that juvenile *L. rhomboides* use as refuge and forage areas (Stoner 1982, 1983). Stomachs of 25 common snook (170–350 mm SL) collected in seagrass habitats in the Indian River Lagoon contained *A. mitchilli*, *L. rhomboides*, and penaeid shrimp as the 3 most abundant prey taxa (Gilmore et al. 1983). These 3 taxa were also the predominant prey consumed by common snook in Charlotte Harbor. In contrast, very few *L. rhomboides* (< 1% of the recorded number of prey) were consumed by common snook in the Ten Thousand Islands (Marshall 1958, Fore and Schmidt 1973), where seagrass is not a predominant habitat type (Sargent et al. 1995).

Common snook were collected from shorelines throughout the Charlotte Harbor estuary; however, we found no significant differences between the diets of small common snook from the east area versus the west area.

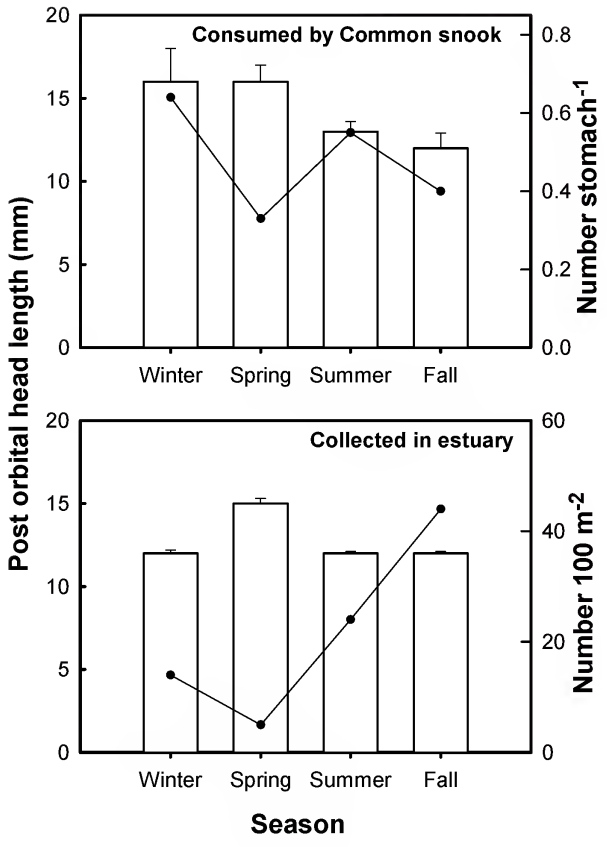

Figure 9. Plot of mean (± standard error) seasonal length (white bars) and abundance (points) for *Farfantepenaeus duorarum* consumed by small common snook (< 550 mm), *Centropomus undecimalis*, and collected in the estuary with 21.3-m shoreline seine. Some SE are too small to be seen.

This may reflect similarities in the shoreline and bottom vegetation—mangrove shorelines and seagrass bottoms dominate the entire western area and cover a majority of the eastern area. These habitats have been shown to support similar fish assemblages throughout Charlotte Harbor (Poulakis et al. 2003). Spatial differences in the diet of common snook between these 2 areas might have been greater if any extraordinary weather events (i.e., hurricanes, floods) had occurred during our sampling period that would have pushed freshwater species into the upper harbor (P.W.S., unpubl. data). Common snook also inhabit rivers, creeks, and backwater marshes, as well as the beaches, inlets, and offshore reefs of the Gulf of Mexico (Volpe 1959, Taylor et al. 1998, R. Novak, University of Florida, pers. comm.) and their diet may differ considerably in these areas, requiring future studies. For example, diet examination from the upper portions of the rivers noted both native and exotic freshwater species as prey for adult common snook (D.A.B., unpubl. data). Also, adult common snook habitat may overlap with those of juveniles in backwater creeks and remote tidal ponds during winter, which can result in low rates of cannibalism (A. Adams, Mote Marine Laboratory, unpubl. data). Our current study, which sampled along estuarine shorelines, did not document any native or exotic freshwater species as prey, nor did it note cannibalism.

This study best describes the diet of common snook 300–550 mm SL; however, adequate data on prey lengths from throughout the size range of common snook were examined to show a significant positive relationship between predator size and prey size. This relationship helps explain why we observed changes in the diet through ontogeny, which has also been observed in juvenile common snook (McMichael et al. 1989, Luczkovich et al. 1995). Small common snook (< 550 mm SL) generally fed on prey of 50–70 mm SL, which coincides with the sizes of some of the most abundant forage fish and small invertebrates collected in the estuary (e.g., cyprinodontids, *Eucinostomus* spp., *F. duorarum*). These abundant small fishes and invertebrates that small common snook are exploiting are apparently too small for larger common snook (≥ 550 mm SL) to consider as prey. The differences we observed between the prey composition of large and small common snook reflect an absence of these small forage fish and invertebrates in the diet of large snook and an increased presence of larger prey, such as *S. foetens*, ariids, and sciaenids, which are abundant in the estuary. Although this was the general pattern we observed, common snook are opportunistic predators that can take advantage of an "easy opportunity" to feed on many small prey items at one time. For example, a 655 mm SL common snook was found with 10 small *Anchoa* spp. in its stomach, which were most likely consumed during an encounter with an entire school. In the estuary, abundant prey that have a wide size range (~ 20–200 mm SL), such as clupeids, *O. chrysoptera*, *L. rhomboides*, and *B. chrysoura* (Nelson 1998, Kupschus and Tremain 2001, Poulakis et al. 2003), were a consistent part of the diets of both small and large common snook.

Differences in the diet of small common snook during winter and summer were strongly linked to their prey-size selectivity. For example, *L. rhomboides* were most important in the diet during summer but virtually absent from the diet during winter. This finding coincides with the recruitment and growth patterns of juvenile *L. rhomboides* in the estuary. *Lagodon rhomboides* recruit to shallow seagrass beds between January and March, at which time they may be too small for common snook to consider as prey. These pinfish reside in the shallow seagrass beds until reaching a size of ca. 80 mm SL between late summer and early winter and then move to deeper water in the bay before migrat-

ing offshore to spawn (Nelson 1998). During summer, the majority of *L. rhomboides* reached a size of ca. 50 mm SL, and it was during this season and at this size when *L. rhomboides* were consumed the most. *Farfantepenaeus duorarum* were important in the diet during all seasons but were most frequently consumed during winter. This species of shrimp has a protracted spawning period and is available throughout the year at sizes of ca. 12–15 mm POHL. *Farfantepenaeus duorarum* may have been more frequent in the diet during winter because of the decreased availability of *L. rhomboides* between 40–75 mm SL. Also, colder water temperatures, which slow the movements of *F. duorarum*, may increase their susceptibility to predation (Fuss and Ogren 1966).

In conclusion, common snook have diverse feeding habits and feed on a wide variety of prey. Evidence shows that they feed throughout the water column and in a variety of habitats, such as mangroves, seagrasses, and unvegetated bottoms. Common snook are opportunistic and exploit prey that are abundant in their environment, yet they appear to be selective in the sizes of prey they consume. Availability of certain-sized prey in the estuary influences what types of prey common snook consume during different stages of their ontogeny, as well as what types of prey they consume seasonally.

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BENTHIC NUTRIENT FLUX IN A SMALL ESTUARY IN NORTHWESTERN FLORIDA (USA)

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ABSTRACT Benthic nutrient fluxes of ammonium (NH_4^+), nitrite/nitrate ($NO_2^- + NO_3^-$), phosphate (PO_4^{-3}), and dissolved silica (DSi) were measured in Escambia Bay, an estuary within the larger Pensacola Bay system of northwestern Florida (USA). Our study occurred during a severe drought which reduced riverine inputs to Escambia Bay. Laboratory incubations of field-collected cores were conducted on 8 dates between June and October 2000 to estimate nutrient flux, and cores were collected from locations exhibiting a range of sediment organic matter content. NH_4^+ flux ranged from − 48.1 to 110.4 μmol m^{-2} h^{-1}, but the mean flux was 14.6 μmol m^{-2} h^{-1}. Dissolved silica (DSi) fluxes were also variable (-109. 3 to 145.3 μmol m^{-2} h^{-1}), but the mean net flux (9.3 μmol m^{-2} h^{-1}) was from the sediment to the water column. Bay sediment fluxes for $NO_2^- + NO_3^-$ and PO_4^{-3} were less variable during this period (− 7.93 to 28.73 and − 1.74 to 3.29 μmol m^{-2} h^{-1} for $NO_2^- + NO_3^-$ and PO_4^{-3}, respectively). Low NH_4^+ fluxes were similar to published estimates from lagoonal Gulf of Mexico (GOM) estuaries, possibly due to the reduced freshwater input. Diminished regeneration of phosphate relative to inorganic nitrogen observed during the study period was consistent with previous research in Pensacola Bay suggesting phytoplankton phosphorus limitation. Finally, the estimated residence time of Escambia Bay and the mean turnover times for NH_4^+ and $NO_2^- + NO_3^-$ suggested that benthic flux significantly influenced nitrogen concentrations in overlying water.

INTRODUCTION

Fluxes of nutrients across the sediment-water interface represent an important link between benthic and pelagic environments (Boynton et al. 1980, Sullivan et al. 1991, Caffrey et al. 1996, Cowan and Boynton 1996), especially in shallow estuarine systems (Kemp et al. 1992, 1998). The benthos can either sequester nutrients from or contribute nutrients to the water column thereby affecting estuarine primary production (Fisher et al. 1982). The environmental and biological factors that regulate benthic nutrient fluxes operate over a variety of temporal and spatial scales (Twilley et al. 1999). For instance, many coastal systems exhibit a seasonal pattern of sediment fluxes, with high summer and low winter fluxes of inorganic nutrients (Kemp and Boynton 1984, Kemp et al. 1998, Cowan et al. 1996). Sediment organic matter (Twilley et al. 1999) and resident benthic fauna (Blackburn and Henrikson 1983, Yamamuro and Koike 1993, Mayer et al. 1995, Gilbert et al. 1998), which can vary over small spatial scales, also influence nutrient fluxes.

Conceptual models of estuarine dynamics, including benthic nutrient fluxes, have emerged from extensive study of temperate estuaries such as San Francisco Bay, Chesapeake Bay, and Narragansett Bay. The 39 estuaries adjacent to the Gulf of Mexico (GOM) differ from temperate estuaries in many ways. For instance, GOM estuaries are generally warmer with less seasonably variable water temperatures, compared to the strong seasonal temperature dynamics of higher latitude systems (Twilley et al. 1999). Furthermore, GOM estuaries have relatively low tidal energy. Tides range up to 1 m in GOM estuaries; however, most systems show tidal ranges from 0.5 to 0.7 m (Solis and Powell 1999). In lieu of reduced tidal influences, the primary forcing function for many GOM estuaries is freshwater input, and GOM estuaries demonstrate a considerable range of freshwater input. River-dominated estuaries include the Atchafalaya/Mississippi River complex (Teague et al. 1988, Solis and Powell 1999), Mobile Bay (Cowan et al. 1996), and Apalachicola Bay (Mortazavi et al. 2000). At the other extreme are the lagoonal estuaries of south Texas, where freshwater input is negligible and evaporation greatly exceeds precipitation and runoff (Flint 1985, Solis and Powell 1999). Furthermore, within a particular system, seasonal or interannual variability in river input will influence the relative role of benthic nutrient flux in estuarine dynamics (Flint 1985, Cowan et al. 1996, Mortazavi et al. 2000). Studies of benthic flux in GOM estuaries over a wide range of physical and ecological conditions will lead to general models of benthic nutrient flux in these systems (Twilley et al. 1999).

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Research on benthic nutrient fluxes in GOM estuaries will also inform studies of coastal eutrophication in the region. Symptoms of eutrophication, including frequent hypoxia/anoxia, loss of submerged aquatic vegetation (SAV), and altered food webs, are prominent in many GOM estuaries (Bricker et al. 1999, Livingston 2001). Benthic flux is an integral component of estuarine nutrient dynamics and thus a potentially strong determinant of coastal eutrophication. For instance, Cowan et al. (1996) found that sediments in Mobile Bay, AL, at times contributed up to 94% of the nitrogen and 83% of the phosphorus required by phytoplankton.

The location for this study was Escambia Bay, FL, a northern GOM estuary. Escambia Bay is part of the Pensacola Bay system, a moderately sized (8800 ha) estuary in northwestern Florida (Figure 1). Escambia Bay, a micro-tidal, partially stratified, drowned river valley estuarine system (Schroeder and Wiseman 1999), has a mean depth of 2.5 m and an approximate tidal range of 0.3 m (Olinger et al. 1975). The primary freshwater input is the Escambia River, with annual flows averaging ca. 195 m^3s^{-1} (Alexander et al. 1996, Solis and Powell 1999). About 80% of the freshwater flow into Pensacola Bay comes from the Escambia River (Olinger et al. 1975). Other freshwater inputs include the Blackwater, Yellow, and East rivers, which empty into the East Bay region. Exchange with the GOM occurs through a narrow, deep pass at the western end of Pensacola Bay and Santa Rosa Sound. The mean water residence time for the entire system is ca. 25 d (Solis and Powell 1999), but the residence time for Escambia Bay

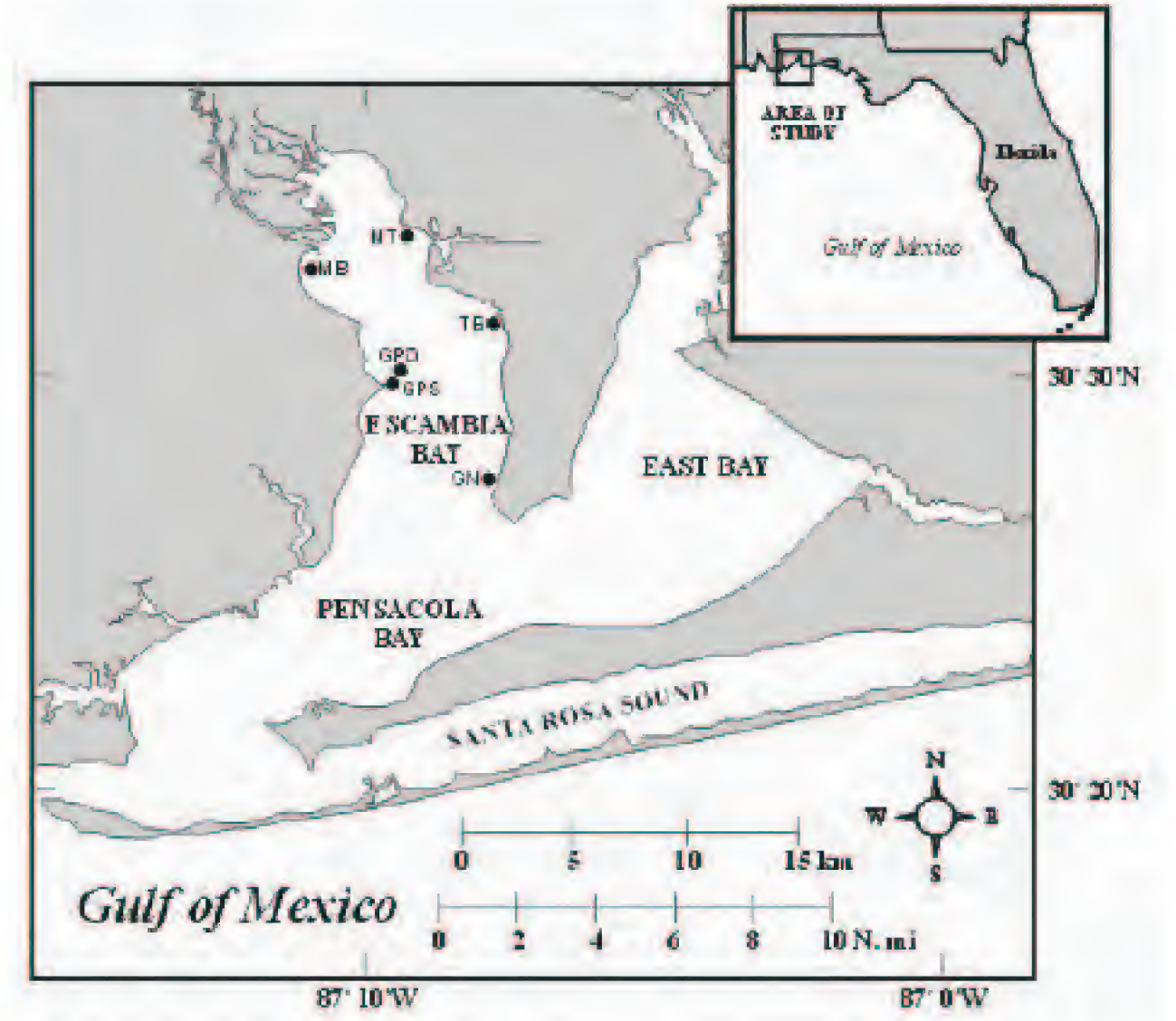

Figure 1. Map of Escambia Bay and the larger Pensacola Bay System. Sampling locations for this study are denoted by the dots and labeled with the following codes: GPS = Gull Point Shallow, GPD = Gull Point Deep, TB = Trout Bayou, MB = Mackie Bay, MT = Mulat Bayou, and GN = Garcon Point.

is between 4 and 8 d (Olinger et al. 1975). Symptoms of eutrophication, including hypoxia and loss of SAV (Olinger et al. 1975, Bricker et al. 1999), have been and are still prominent in this estuary (Livingston 2001). The primary objective of this research was to quantify benthic fluxes of inorganic nutrients (NH_4^+, $NO_2^- + NO_3^-$, PO_4^{-3}, and DSi) in Escambia Bay. In addition to nutrient flux measurements, we estimated the relative importance of benthic nutrient flux to overlying water column concentrations in Escambia Bay by estimating turnover times.

MATERIALS AND METHODS

Field Collection and Laboratory Methods

Nutrient flux measurements were made 8 times between June and October 2000 (Table 1) using diver-collected cores incubated in the laboratory under flow-through conditions (Miller-Way et al. 1994, Miller-Way and Twilley 1996). Collection sites were all unvegetated, and sediment organic matter content ranged between 0.44% and 8.21% (Table 1). Core cylinders (15 cm i.d.) were 30 cm high, and cylinders were pressed into the sediments to a depth of 15 to 20 cm. The top of each core cylinder was sealed to create a vacuum, and cores were carefully removed from the sediment. To prevent sediment slumping, a plastic plate with the same diameter as the cylinder was placed under the sediment plug. Following collection, the bottom of each core was sealed with a PVC cap fitted with an O-ring gasket. Tops were placed on the cores for transport in insulated coolers to the laboratory. Water (100 L) was collected from each site using a diaphragm pump, filtered through an 80-µm mesh, and stored in 20-L polyethylene carboys (Nalgene®). On the first 2 collection dates, water was collected from the top 0.5 m, but on the remaining dates water was collected from the bottom 0.5 m. Standard hydrographic parameters (temperature, dissolved oxygen, pH, and salinity) were measured at the surface and bottom of each site with a HydroLab®.

In the lab, overlying water in the cores was drained and replaced with site water. Cores were then sealed, placed in a water bath, and incubated in the dark. Water bath temperature was adjusted over the study to mimic ambient field temperatures (± 1 °C) measured on station. Site water was delivered at a controlled rate via a peristaltic pump (MasterFlex®) to each core chamber through Tygon® tubing. Preliminary experiments demonstrated that flow rates ca. 10 mL min^{-1} were suitable for estimating nutrient fluxes. Water entered each core through an inflow port in the lid via a cannula fitted with a rubber stopper and drained out a separate port in the lid. Gentle internal stirring was maintained using a floating stir bar (Nalgene®) mounted to the chamber top and propelled by a magnetic stirrer. Stirring was intended to minimize the development of chemical gradients within experimental chambers (Miller-Way 1994).

Nutrient concentrations from inflow and outflow water were used to calculate flux. Outflow water was sampled directly from each core; inflow nutrient concentrations were determined from the source water (Miller-Way 1994, Miller-Way and Twilley 1996). Samples were collected in acid-washed glass bottles at 2.5–3.5 h intervals

TABLE 1

Sample dates and physical/chemical characteristics of sampling sites in Escambia Bay, FL. For study sites, Gull Point SH and DP indicate shallow and deep sites, respectively, near Gull Point. [1]determined as weight loss on ignition, [2]measured using an Elementar Vario EL without acidification, [3]molar ratio, [4]no data.

Date	Site	Depth (m)	Temp (°C)	DO (mg L^{-1})	Sal (PSU)	% organic[1]	%C[2]	%N[2]	C:N[3]	NH_4^+ (µM)	NO_2^-+NO_3^- (µM)	PO_4^{-3} (µM)	DSi (µM)
6/6/2000	Gull Point SH	1.0	27.6	7.8	17.3	0.50	0.12	0.01	14.23	0.27	0.03	0.11	56.85
	Gull Point DP	2.0	27.8	7.3	19.1	6.95	1.70	0.14	14.36				
6/20/2000	Trout Bayou	2.0	29.4	5.0	17.5	0.44	0.08	0.02	6.72	0.79	0.56	0.01	47.52
7/12/2000	Mackey Bay	1.0	31.3	5.3	17.3	0.61	0.13	0.02	9.66	3.01	0.16	1.00	67.60
7/26/2000	Mulat Bayou	1.0	29.7	n.d.[4]	19.1	2.27	0.71	0.08	10.54	1.38	0.21	0.74	58.80
8/29/2000	Gull Point SH	1.0	31.0	3.2	26.6	0.44	n.d.	n.d.	n.d.	3.15	0.64	0.67	49.20
	Gull Point DP	2.0	30.9	3.5	25.1	8.21	2.43	0.22	13.01				
9/19/2000	Mackey Bay	0.8	25.3	5.2	19.3	0.59	0.23	0.04	8.61	4.49	2.97	0.30	53.63
10/16/2000	Garcon Point	1.6	21.9	5.6	31.2	0.60	0.13	0.03	6.69	1.98	0	0.08	7.93
10/30/2000	Gull Point SH	0.7	23.1	7.1	23.9	0.55	0.13	0.02	7.57	4.32	0.29	0.15	21.42
	Gull Point DP	2.0	23.1	7.1	24.0	7.99	2.19	0.20	12.50				

and stored on ice until processing within 1 h. Samples were filtered through a pre-combusted Whatman® GF/F filter, and the filtrate was collected in HDPE bottles and frozen at −70 °C until nutrient analyses. Experiments lasted 10–12 h, during which time 5 serial samples were collected from each core (only 4 time points were sampled on the first date). At the conclusion of each experiment, 1–2 cores from each site were selected for sediment analysis. Three sediment subsamples, taken from the top 5 cm using an open-ended 60 mL syringe, were pooled and stored at 4 °C. Small amounts (2–5 g) were dried and combusted at 500 °C for 4 h to determine %organic matter [determined as weight loss on ignition (WLOI)]. In addition, sediment %carbon (C) and %nitrogen (N) were measured on samples without acidification using an Elementar® vario EL Analyzer.

All nutrient analyses were conducted on an Astoria Pacific® analyzer following US EPA standard methods (US EPA 1984). NH_4^+ was analyzed using the indolphenol blue method. NO_2^- and NO_3^- were analyzed together by the cadmium reduction method, and throughout this paper both oxidized forms of nitrogen are referred to collectively as $NO_2^- + NO_3^-$. PO_4^{-3} was analyzed as orthophosphate using the molybdenum method, and DSi was measured via ß-molybdosilicate formation.

Flux Calculations and Statistical Analyses

Fluxes were calculated for each nutrient using the formula:

$$\text{Flux} = F(C_o - C_i) / A,$$

where F = flow rate (L h^{-1}), C_o = outflow concentration (µM), C_i = inflow concentration (µM), and A = benthic surface area (m^2). Flux (µmol m^{-2} h^{-1}) was calculated for each nutrient at each sampling interval. Sediment disturbance was minimized, but as a rule initial flux estimates (i.e., determined from initial C_o and C_i values) were excluded from analyses. Flux for each nutrient was calculated as the mean of the individual core time point estimates. By convention, a positive flux value represents nutrient efflux from the sediment, while a negative flux denotes influx into the sediment. The overall mean flux rate for a parameter was calculated as the mean of all measurements.

To examine local variability in fluxes, cores were collected from 2 depths at Gull Point (Table 1, Figure 1) on 3 dates (6 June, 29 August, and 30 October). Sediment at the shallower Gull Point site was similar to other sampled shallow habitats, but the deeper site was representative of the muddy habitat that comprises ca. 75% of Escambia Bay (Olinger et al. 1975). To test whether fluxes were significantly different across depth, data from these experiments were analyzed using repeated measures ANOVA (rmANOVA, Potvin et al. 1990, Von Ende 1993). The rmANOVA followed a split-plot single factor design, with depth and time representing the between- and within-subject factors, respectively (Potvin et al. 1990). The assumptions of normality and homoscedasticity were tested, and log-transformations were used to correct significant heteroscedasticity. If data could not be made homoscedastic, a nonparametric test of the overall treatment effect was done using a Wilcoxon two-sample test (Potvin et al. 1990). All analyses were done using SAS (SAS 1989).

Pearson product-moment coefficients were calculated to examine the relationships among mean nutrient fluxes, water column nutrient concentrations, and hydrographic and sediment characteristics [temperature, dissolved oxygen (DO), pH, salinity, sediment %organic matter, sediment %C content, sediment %N content, sediment C:N molar ratios].

Nutrient turnover times were used to evaluate the overall importance of the benthos as a source or sink of dissolved nutrients for this shallow estuary. Turnover time (d) was calculated using overlying water column concentrations, water depth, and sediment flux estimates (Warnken et al. 2000); these estimates were compared to the residence time reported for Escambia Bay (Olinger et al. 1975).

Results

Water temperature over the survey period followed a typical seasonal pattern, ranging from 31 °C in July and August to 22 °C in October (Table 1). On all sampling dates, DO was high (> 5 mg L^{-1}), with the exception of 29 August, when it was nearly 3 mg L^{-1}. The high salinity (> 17 PSU) was atypical and reflected the extreme drought and consequent reduced freshwater input from the Escambia River during this period. Sediments demonstrated variable particle size distributions, from very coarse sands to fine silts and muds, and the organic content of the sediments (determined as WLOI) ranged from less than 1% up to ca. 8%. The deeper site off Gull Point consistently had the highest sediment organic matter. Sediment C:N molar ratios ranged from 6.7 at Garcon Point to 14.4 at the deeper Gull Point site (Table 1).

NH_4^+ flux estimates ranged from − 48.1 to 110.4 µmol m^{-2} h^{-1} (Table 2), and the mean flux indicated overall efflux of NH_4^+ (14.6 µmol m^{-2} h^{-1}). The highest NH_4^+ fluxes were observed on 26 July and 29 August (at the deep station). On the final 3 sampling dates, however, results indicated NH_4^+ influx to the sediment (Figure 2).

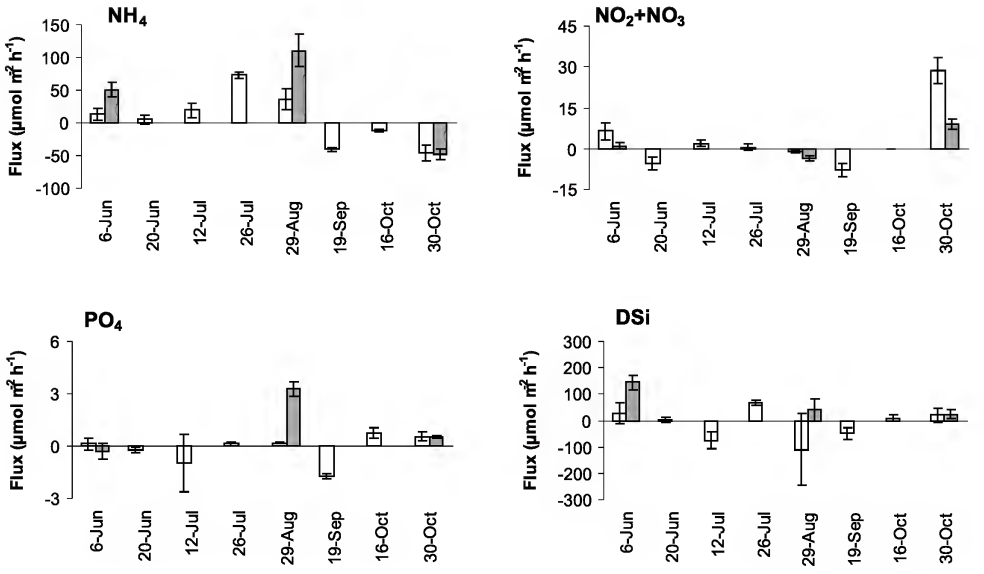

Figure 2. Nutrient fluxes (µmol m-2 h-1) as measured 8 times between June and October, 2000, in Escambia Bay, FL. Bars are means of replicate cores, and error bars are ±1 SE. Experiments on 6 June, 29 August, and 30 October at Gull Point were done at shallow (open bars) and deep (gray bars) locations.

Over the study, NH_4^+ flux was positively correlated with water temperature ($P = 0.0063$, Table 3); the influx of NH_4^+ into the sediments occurred only late in the season when water temperatures fell to 25 °C and below. When a direct comparison was made between the shallow sandy and deep muddy Gull Point sites, NH_4^+ flux was typically higher at the muddy site. There was a marginal statistical difference (rmANOVA, $P = 0.058$, Figure 2) between NH_4^+ fluxes at the 2 depths in the 6 June experiment. A significant Time × Treatment interaction ($P < 0.01$) indicated a difference across depth for NH_4^+ flux on the 29 August experiment. On the final sampling date, though, NH_4^+ flux estimates were similar at both depths.

The pattern of $NO_2^- + NO_3^-$ flux differed from NH_4^+. $NO_2^- + NO_3^-$ fluxes were low in Escambia Bay over the survey period, ranging from − 7.9 to 28.7 µmol m^{-2} h^{-1}, with a mean flux of 2.7 µmol m^{-2} h^{-1} (Table 2). $NO_2^- + NO_3^-$ fluxes into sediments were apparent on 20 June, on 29 August at both depths, and 19 September. $NO_2^- + NO_3^-$ efflux into the water column occurred on 6 June

TABLE 2

Mean (S.E.) nutrient fluxes from locations in Escambia Bay, FL, measured from intact core incubations during Summer/Fall, 2000. Rates given in µmol m^{-2} h^{-1}.

Date	Site	N	NH_4^+		$NO_2^-+NO_3^-$		PO_4^{-3}		DSi	
6/6/2000	Gull Point SH	3	13.0	(9.4)	6.4	(3.0)	0.1	(0.4)	27.5	(41.1)
	Gull Point DP	3	50.7	(11.1)	0.9	(1.2)	-0.3	(0.4)	145.3	(26.9)
6/20/2000	Trout Bayou	4	5.0	(7.1)	-5.4	(2.4)	-0.2	(0.2)	1.3	(9.9)
7/12/2000	Mackey Bay	4	19.5	(11.3)	1.9	(1.2)	-1.0	(1.7)	-74.8	(32.0)
7/26/2000	Mulat Bayou	4	73.4	(5.0)	0.5	(1.2)	0.1	(0.1)	67.5	(10.8)
8/29/2000	Gull Point SH	2	35.7	(16.2)	-1.2	(0.6)	0.2	(0.0)	-109.3	(134.3)
	Gull Point DP	4	110.4	(25.4)	-3.5	(0.9)	3.3	(0.4)	39.8	(39.8)
9/19/2000	Mackey Bay	3	-40.9	(3.9)	-7.9	(2.4)	-1.7	(0.1)	-49.3	(21.0)
10/16/2000	Garcon Point	4	-12.0	(1.8)	0.0	(0.0)	0.8	(0.3)	8.7	(11.7)
10/30/2000	Gull Point SH	4	-45.7	(11.7)	28.7	(4.8)	0.6	(0.3)	21.1	(28.2)
	Gull Point DP	4	-48.1	(7.2)	8.9	(1.8)	0.5	(0.1)	24.1	(16.6)
	Average		14.6		2.7		0.2		9.3	

TABLE 3

Pearson product-moment correlation coefficients between benthic fluxes and environmental parameters. Temp, pH, DO, and Sal are all environmental parameters, while %organic, %C, %N, and C:N refer to various sediment characteristics. [Nutrient] refers to the nutrient concentration in the overlying water. $N = 11$ for all pairs, except %C, %N, and C:N, where $N = 10$. $^{**}P < 0.01$, $^{*}0.05 > P > 0.10$

	NH_4^+ Flux	$NO_2^- + NO_3^-$ Flux	PO_4^{-3} Flux	DSi Flux
Temp	0.763**	– 0.468	0.067	– 0.19
pH	– 0.169	0.586*	0.328	– 0.036
DO	– 0.486	0.569*	– 0.266	0.587*
Sal	– 0.11	0.16	0.544*	– 0.212
%organic	0.361	– 0.047	0.541*	0.580*
%C	0.421	– 0.096	0.594*	0.516
%N	0.408	– 0.127	0.602*	0.47
C:N	0.464	– 0.037	0.231	0.550*
[NH_4]	– 0.449	0.276	0.029	– 0.503
[NO_2+NO_3]	– 0.273	– 0.403	– 0.389	– 0.382
[PO_4]	0.536*	– 0.221	0.063	– 0.408
[Si]	0.541*	– 0.449	– 0.321	– 0.059

and 30 October (Figure 2). $NO_2^- + NO_3^-$ efflux on 30 October corresponded to the significant influx of NH_4^+ during that experiment, implying that NH_4^+ influx provided substrate for nitrification at this time. With respect to environmental characteristics, there was a weak relationship between $NO_2^- + NO_3^-$ flux and DO ($P = 0.086$, Table 3).

Like $NO_2^- + NO_3^-$, fluxes of PO_4^{-3} in Escambia Bay were generally low (– 1.7 to 3.3 μmol m^{-2} h^{-1}; Table 2). PO_4^{-3} flux estimates were negligible in all measurements through July. On 29 August there was a significant PO_4^{-3} efflux at both depths, and flux at the deeper site was significantly higher (rmANOVA, $P < 0.01$) than at the shallow location. PO_4^{-3} fluxed into the sediment during the 19 September experiment but fluxed out in both October tests (Table 2, Figure 2). On average, Escambia Bay sediments showed a positive net flux (0.2 μmol m^{-2} h^{-1}). Statistical analyses suggested relationships between PO_4^{-3} flux and sediment %C, sediment %N, %organic, and salinity (Table 3).

TABLE 4

Turnover times (d) of nutrients in Escambia Bay, FL, calculated from flux data, overlying water nutrient concentrations, and water depth.

	NH_4^+	NO_2^-+NO_3^-	PO_4^{-3}	DSi
Average	3.9	4.3	77.6	273.6
Range	0.4–3.1	0.2–16.2	7.1–271.1	29.6–3018.6

Dissolved silica fluxes were variable (– 109.3 to 145.3 μmol m^{-2} h^{-1}), and mean DSi flux over this survey was positive (9.3 μmol m^{-2} h^{-1}, Table 2). The highest DSi flux was observed on 6 June at the deep site, and there was also a strong positive flux on 26 July (Table 2, Figure 2). A silica influx was detected at the Mackey Bay site on 12 July (– 74.8 μmol m^{-2} h^{-1}) and 19 September (– 49.3 μmol m^{-2} h^{-1}). All other DSi fluxes were indistinguishable from 0. Marginal correlations existed between DSi flux and %organic matter ($P = 0.062$), sediment C:N ratio ($P = 0.0992$), and DO ($P = 0.075$; Table 3).

Nutrient turnover times in Escambia Bay ranged from < 1 d up to 13 d for NH_4^+ and < 1 d up to 16 d for $NO_2^- + NO_3^-$ (Table 4). The mean turnover time was 3.9 d for NH_4^+ and 4.3 d for $NO_2^- + NO_3^-$. Mean turnover times for the other nutrients were much longer (PO_4^{-3}:78 d; DSi: 274 d). Olinger et al. (1975) reported a 4–8 d residence time for Escambia Bay, depending on the freshwater input. US Geological Survey (USGS) streamflow data collected from the Escambia River at Century, FL (http://water.usgs.gov/nwis/discharge) demonstrated that Escambia River discharge was severely reduced during 2000 (Figure 3). In fact, the discharge was the lowest recorded in 65 years. Because of the extremely low freshwater input during summer 2000, it is highly likely that a 4–8 d residence time underestimates the residence time during the study period. If that were correct, then water residence time was likely greater than the turnover times for inorganic nitrogen, but still shorter than those of PO_4^{-3} and DSi.

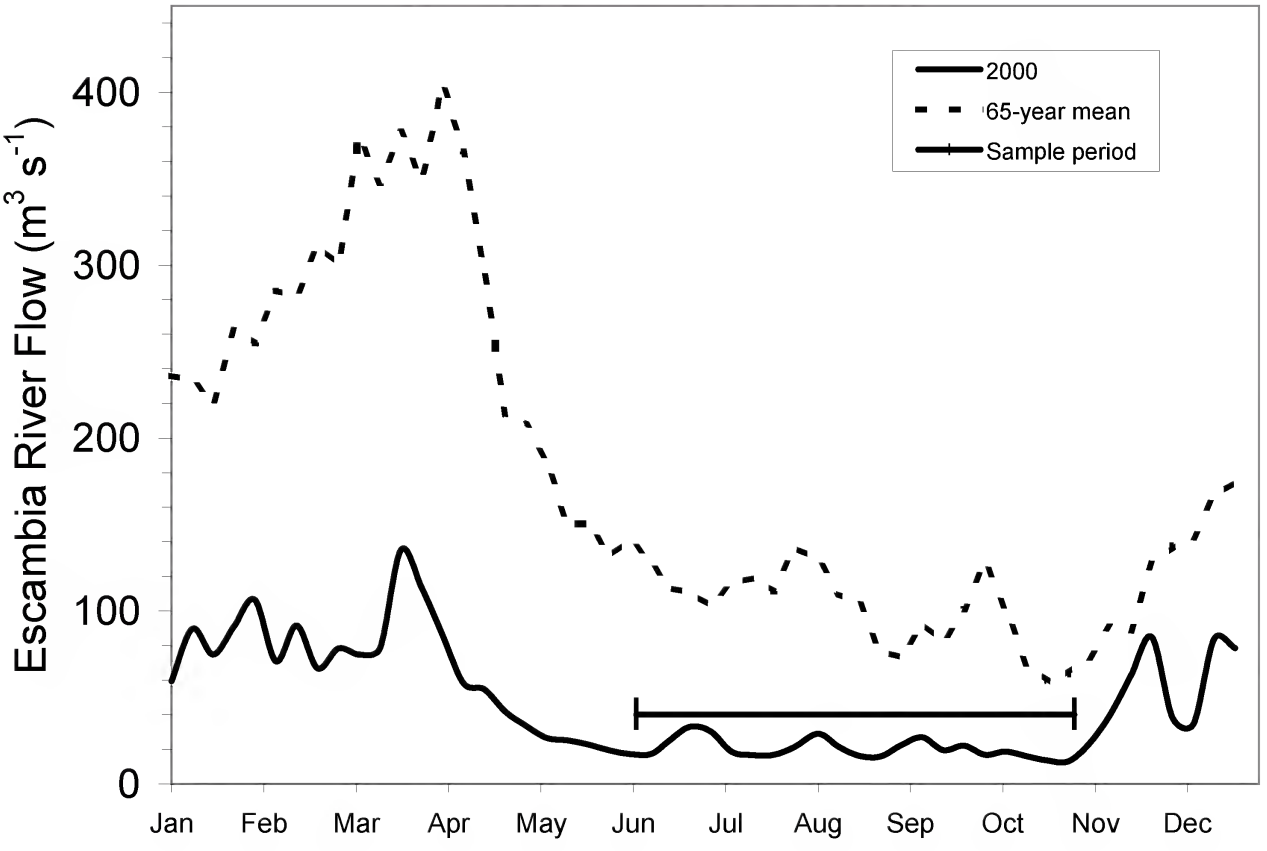

Figure 3. Hydrograph for the Escambia River discharge ($m^3 s^{-1}$). The solid line shows the discharge from 2000, whereas the dashed line shows the historical mean weekly flow averages. The horizontal bar indicates the period during which benthic flux studies occurred.

DISCUSSION

In general, estuaries of the GOM are river-dominated, that is, freshwater input is the dominant forcing function in these systems (Twilley et al. 1999). During the period of this study, though, the major source of freshwater input for Escambia Bay was only ca. 15% of its 65-year average. During this low-flow period, the benthic fluxes for many of the parameters resembled those witnessed in GOM lagoonal and other low input systems, rather than the typical river-dominated estuaries.

NH_4^+ fluxes observed in this study demonstrated a larger range of variation (– 48.1 to 110.4 μmol $m^{-2} h^{-1}$) than previously studied Texas lagoons (Trinity-San Jacinto, – 3.9 to 45.2 μmol $m^{-2} h^{-1}$; Nueces, 0.6 to 7.0 μmol $m^{-2} h^{-1}$). However, the mean NH_4^+ flux in Escambia Bay (14.6 μmol $m^{-2} h^{-1}$) was more similar to estimates from the Trinity-San Jacinto (11.7 μmol $m^{-2} h^{-1}$, Zimmerman and Benner 1994), Nueces estuaries (2.9 μmol $m^{-2} h^{-1}$, Yoon and Benner 1992), and Ochlockonee Bay (1.3 μmol $m^{-2} h^{-1}$, Seitzinger 1987), a small riverine system in Florida, compared to the larger river-dominated systems of Apalachicola Bay, Mobile Bay, and Fourleague Bay (NH_4^+ fluxes of 38.0, 62.8 and 141.7 μmol $m^{-2} h^{-1}$, respectively; Twilley et al. 1999). These latter systems are characterized by freshwater input of nearly an order of magnitude higher than other GOM systems (Solis and Powell 1999). Higher freshwater input delivers more inorganic nutrients fueling primary production; subsequent decomposition in the sediment often leads to higher NH_4^+ fluxes. During the extended period of drought and reduced freshwater input, NH_4^+ fluxes measured in Escambia Bay resembled the lagoonal and smaller input GOM systems.

Reduced freshwater input may have influenced NH_4^+ fluxes, but many other factors, like temperature, sediment organic content, and macroinvertebrate assemblages, also impact sediment NH_4^+ flux. Temperature influenced NH_4^+ flux, as suggested by the strong positive correlation between these variables (Table 3), and this is a common result from other studies (e.g., Teague et al. 1988). Our data did not indicate a general relationship between NH_4^+ flux and sediment organic matter content seen in other systems (e.g., Cowan et al. 1996). However, data collected from shallow and deep Gull Point sites often showed high-

er NH_4^+ (and other nutrient) fluxes at the deeper, more organic-rich location (Table 2, Figure 2). Higher organic matter content provides substrate for higher remineralization rates. Flux differences were not evident in all Gull Point comparisons, however, and this suggests that localized factors, for instance benthic invertebrate assemblages, further modified nutrient fluxes. Benthic macroinvertebrates can impact fluxes directly by excreting NH_4^+ (Yamomura and Koike 1993) or indirectly via bioturbation (Miller-Way 1994). Macroinvertebrate communities in Escambia Bay vary with sediment type (Olinger et al. 1975). One sediment core from both the shallow and deeper locations collected on 6 June was sieved following the test. At the deeper, high-organic matter site, polychaetes (e.g., *Mediomastus* sp.) were more abundant than at the lower organic matter site (1500 vs. 556 m^{-2}, respectively). Polychaetes influence sediment nitrification and denitrification (Pelegri and Blackburn 1995), and community differences across different sediment types were likely contributors to nutrient flux variability (Twilley et al. 1999).

Benthic $NO_2^- + NO_3^-$ fluxes in Escambia Bay averaged 2.7 μmol m^{-2} h^{-1} and were similar to $NO_2^- + NO_3^-$ fluxes in Ochlockonee Bay (1.1 μmol m^{-2} h^{-1}, Seitzinger 1987) and the Trinity-San Jacinto system (– 2.7 μmol m^{-2} h^{-1}, Zimmerman and Benner 1994). In the present study, there was no apparent relationship between $NO_2^- + NO_3^-$ flux and its concentration in the bottom-water. Sediments are thought to act as $NO_2^- + NO_3^-$ sinks when ambient concentrations are high (Boynton et al. 1980, Teague et al. 1988, Jensen et al. 1990, Cowan and Boynton 1996, Trimmer et al. 1998). The low mean $NO_2^- + NO_3^-$ concentrations (0.6 μM, Table 1) in Escambia Bay during this study would be unlikely to drive $NO_2^- + NO_3^-$ dynamics at the sediment-water interface.

Other factors, including nitrification in the sediments, will regulate $NO_2^- + NO_3^-$ flux. The potential for sediment nitrification depends on sediment NH_4^+ concentration and local fauna (Mayer et al. 1995). We did not measure porewater nutrient concentrations, but the significant influx of NH_4^+ measured during the final 3 collection dates could have provided the necessary substrate for high nitrification rates. The strong net efflux of $NO_2^- + NO_3^-$ on 30 October corresponded to a strong influx of NH_4^+ (Table 2, Figure 2), implying that NH_4^+ uptake may have driven significant nitrification in this system. Additionally, during incubations showing significant NH_4^+ influx, the results did not reveal an equivalent molar efflux of $NO_2^- + NO_3^-$ (Table 2), suggesting that some nitrogen may have been lost from the system via denitrification. We did not measure denitrification in Escambia Bay, but previous research suggested potential denitrification rates could be very high (Flemer et al. 1998). Denitrification has been documented as a sink for nitrogen in other GOM estuaries (Seitzinger 1987, Yoon and Benner 1992, Zimmerman and Benner 1994). Denitrifying organisms utilize nitrate in the overlying water, but they also rely on nitrification in the sediment to produce NO_3^- for denitrification (Gardner et al. 1987, Yoon and Benner 1992). Denitrification in this system could be fueled in part by sediment NH_4^+ uptake.

Elderfield et al. (1981), Boynton et al. (1991), and Cowan and Boynton (1996) reported high benthic PO_4^{-3} fluxes in northeastern US estuaries, but PO_4^{-3} fluxes in GOM estuaries are typically low (Twilley et al. 1999). Mean benthic PO_4^{-3} flux (0.2 μmol m^{-2} h^{-1}) in Escambia Bay was similar to that from the Trinity-San Jacinto estuary (0.6 μmol m^{-2} h^{-1}, Zimmerman and Benner 1994). Furthermore, the range of PO_4^{-3} flux in Escambia Bay (– 1.7 to 3.3 μmol m^{-2} h^{-1}) is similar to that of the Trinity-San Jacinto (– 2.6 to 3.5 μmol m^{-2} h^{-1}, Zimmerman and Benner 1994) and much less variable than most other GOM systems (Twilley et al. 1999). In the Guadalupe and Nueces estuaries, the sediments tend to be PO_4^{-3} sinks (Twilley et al. 1999), whereas Mobile Bay and Mississippi River Bight sediments are PO_4^{-3} sources (3.9 and 17.5 μmol m^{-2} h^{-1}, respectively). PO_4^{-3} efflux often accompanies reduced DO, and Cowan et al. (1996) hypothesized that this is associated not only with DO concentration but also with the duration that sediments are exposed to hypoxic/anoxic conditions. The highest PO_4^{-3} efflux in our study coincided with a period of lower DO in the bottom waters (< 3.5 mg L^{-1}, Table 1).

Relative fluxes of nitrogen and phosphorus from this study indicate another important aspect of benthic flux dynamics in Escambia Bay. Assuming that organic matter deposited to the sediments follows the Redfield ratio of 16:1 N:P and that this material is the primary substrate for remineralization, we would expect that the total fluxes of DIN and DIP will approximate Redfield. However, the mean DIN:DIP ratio calculated from our results (86.5) far exceeded the Redfield ratio, suggesting that sediments were retaining phosphorus. Sediment phosphorus binding appeared to be important, if temporally variable, in Mobile Bay (Cowan et al. 1996), and Caffrey et al. (1996) argued that phosphorus binding might be occurring in San Francisco Bay sediments as well.

The implications of reduced phosphorus regeneration in Escambia Bay extend to local phytoplankton dynamics. A previous study in Pensacola Bay using nutrient bioassays found phosphorus-limited phytoplankton growth, especially during summer (Murrell et al. 2002). N:P ratios of material arriving via the Escambia River often exceed 16 (Alexander et al. 1996), and low PO_4^{-3} remineralization

from the sediments may contribute to or even exacerbate phosphorus limitation within Pensacola Bay. In contrast, Cowan and Boynton (1996) argued that sediment fluxes were consistent with a model of phytoplankton limitation in the Chesapeake Bay system: the phytoplankton was nitrogen-limited in the summer when benthic fluxes showed increased regeneration of phosphorus relative to nitrogen.

DSi fluxes were variable in our study (Table 2, Figure 2), and similar variability (342 to -15 μmol m^{-2} h^{-1}) was observed in Mobile Bay by Cowan et al. (1996). Many factors influence silica fluxes, including temperature, sediment character, and benthic flora and fauna (Sundbäck et al. 1991, Cowan et al. 1996, Sigmon and Cahoon 1997). With respect to sediment character, our results suggested a weak relationship between DSi flux and %organic matter ($P = 0.0616$, Table 3), a finding consistent with the results of Sigmon and Cahoon (1997). We did not estimate benthic algal biomass, but benthic diatoms can act as silica sinks under both dark and light conditions (Sundbäck et al. 1991, Sigmon and Cahoon 1997). Benthic invertebrates, like polychaetes, can also impact DSi fluxes (Marinelli 1992). As previously noted, polychaetes were more abundant at the deeper site, where silica flux was higher than at the shallow location on 6 June. Such quantitative differences between invertebrate communities across the depth gradient may have influenced silica dynamics at that time.

These results also suggest that benthic flux can represent a strong link between the benthic and pelagic habitats of Escambia Bay, FL, as ascertained from nutrient turnover times. Both NH_4^+ and $NO_2^- + NO_3^-$ showed turnover times (Table 4) equal to or less than the residence time of the Bay (4–8 d), implying that benthic exchange processes can affect the overlying nitrogen concentrations before water is advected. This is common in shallow estuarine systems (Kemp et al. 1998, Warnken et al. 2000). The estimated turnover times of PO_4^{-3} and DSi were much longer (78 and 274 days, respectively, Table 4), and thus the influence of benthic processes on water column concentrations of PO_4^{-3} and DSi is likely more limited. Further study of benthic fluxes in this estuary will provide estimates of turnover time under a wider variety of environmental conditions. Turnover time is calculated from water column concentrations, sediment flux rates, and water depth (Warnken et al. 2000). Water depth is relatively static, but flux rates and water column concentrations will change with varying freshwater input. Continued research in Escambia Bay has documented the dynamic distribution of inorganic nutrients with changing freshwater input (*pers. comm.*, M.C. Murrell, US EPA, Gulf Breeze, FL).

Another goal of continued research on benthic flux in this system will be estimating the relative contributions of nutrients from benthic and riverine sources. In some systems, the benthic contribution to estuarine nutrient pools can equal or exceed the supply from riverine or other external sources (Nixon 1981, Fisher et al. 1982). For example, Flint (1985) reported that sediment NH_4^+ flux in Corpus Christi Bay, TX, provided greater than 90% of the nitrogen necessary for primary production. Similarly, Mortazavi et al. (2000) showed that, during low-flow summer periods (May–September), benthic flux in Apalachicola Bay supplied nitrogen (in the form of NH_4^+) to the water at about the same rate as the Apalachicola River. This finding of Mortazavi et al. (2000) also implies that the benthic contribution to estuarine nutrient levels may change over longer temporal scales. Seasonal dynamics (low-flow summer, high-flow spring) are overlain by regional climactic events, like droughts, that introduce variability over longer periods. The mean summer discharge from the Escambia River is 138 m^3 s^{-1}. Discharge during 2000 was dramatically lower than the 65-year mean (Figure 3). From these data it is difficult to extrapolate a system-wide nutrient budget for Escambia Bay; the spatial and temporal distribution was limited and the study occurred during a unique period. Only continued research on this topic can quantify the relative contributions of nutrient sources in this system.

Our study of benthic nutrient flux in Escambia Bay, a northern GOM estuary, occurred during a period of regional drought and low freshwater input. The mean daily flow of the Escambia River during our study was the lowest ever recorded and only 15% of the long-term mean summer daily flows. Low riverine input, and consequent low nutrient loading, is associated with reduced benthic nutrient fluxes in GOM estuaries (Twilley et al. 1999). Our NH_4^+ flux data from Escambia Bay were consistent with that general observation. Flux of PO_4^{-3} was also very low, a condition typical of GOM estuaries (Twilley et al. 1999). More importantly with respect to system dynamics, PO_4^{-3} may not be remineralized from the benthos to the water column at the rate it is supplied. Previous observations in Pensacola Bay showed phytoplankton phosphorus-limitation, and reduced sediment PO_4^{-3} flux likely contributed to this condition. Further research is necessary to quantify the contribution of benthic flux to Escambia Bay nutrient dynamics over a wider range of freshwater inputs.

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Body Size of the Endosymbiotic Pea Crab *Tumidotheres maculatus*: Larger Hosts Hold Larger Crabs

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BODY SIZE OF THE ENDOSYMBIOTIC PEA CRAB *TUMIDOTHERES MACULATUS*: LARGER HOSTS HOLD LARGER CRABS

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ABSTRACT The endosymbiotic pea crab, *Tumidotheres maculatus*, uses a broad range of host taxa, including several bivalve species, in the northern Gulf of Mexico. Because shelter size affects the size of other, free-living crab species, we hypothesized that pea crabs living in larger bivalve hosts should attain larger sizes. Crabs and hosts collected from 3 field sites in northern Florida show this trend. We examined crabs living in a large host, the pen shell *Atrina rigida*, and found them to be larger than pea crabs living in a small host, the bay scallop *Argopecten irradians*. Moreover, this trend was only apparent among female pea crabs, which are lifelong endosymbionts, but not among males, which are free-ranging and move among hosts. Our data support the broader conclusion that shelter size influences adult crab size in brachyuran crabs.

INTRODUCTION

The pea crab (*Tumidotheres maculatus*) is an endosymbiont that has been found in many different species of hosts. At least half of these hosts are bivalves (Derby and Atema 1980, Bierbaum and Ferson 1986). The pea crab (reassigned from the genus *Pinnotheres* by Campos (1989) for morphological reasons) has "dwarf" males that rarely exceed 6 mm across the carapace, move freely from host to host, and are able to feed independently of the host (Sastry and Menzel 1962, Bierbaum and Ferson 1986). Female pea crabs grow much larger, pass through 7 distinct developmental stages (Pearce 1964, Campos 1989), and live their entire adult lives within a host (Bierbaum and Ferson 1986). By clinging to the gills of the host with their legs, they use their chelae to pick up mucous food strands aggregated by the host (Bierbaum and Ferson 1986, Bierbaum and Shumway 1988). This symbiotic relationship is believed to be either commensal or parasitic (Bologna and Heck 2000). Common bivalve hosts in the northeastern Gulf of Mexico include the bay scallop (*Argopecten irradians*), the pen shell (*Atrina rigida*), and the mussel (*Modiolus americanus*).

The prevalence of pea crabs in bivalve populations appears to vary widely. Sastry and Menzel (1962), working in Florida, found that infestation rates of pea crabs ranged from 20% to more than 47% in bay scallops collected between October 1957 and November 1958. Pearce (1964) reported that 97.6% of mussels, *Mytilus edulis*, in Quicks Hole, Massachusetts, were infested with pea crabs. Bierbaum and Shumway (1988) found that 69% of mussels from a bed in Martha's Vineyard, Massachusetts, were infested with pea crabs. In St. Joseph Bay, Florida, Bologna and Heck (2000) found that the infestation rate of bay scallops by pea crabs ranged from 0% to more than 20% from 1994 to 1996. In none of these studies did variations in pea-crab infestation rates appear to be seasonal.

Within an individual host bivalve, endosymbiont infestation may vary in 2 ways: 1) variation in the number of pea crabs per host and 2) variation in the size of female crabs. Crab size can be influenced by environmental factors, such as shelter size, among non-symbiotic brachyuran crabs. Kuhlmann and Walker (1999) found strong and significant size differences between 2 populations of the spineback hairy crab, *Pilumnus sayi*, in the northeastern Gulf of Mexico, and they showed that the difference in crab sizes between the 2 populations was due to differences in the sizes of available shelter at the 2 locations. Likewise, Beck (1995) showed that in populations of the stone crab, *Menippe adina*, crabs molted and spawned more often when large PVC pipe shelters were provided. However, a relationship between host size and symbiont size has not yet been demonstrated for symbiotic crabs such as the pea crab, despite the fact that potential bivalve hosts for this crab vary greatly in size.

We hypothesized that pea crabs living in larger host species might grow to larger sizes than pea crabs in smaller bivalve hosts. Mussels and bay scallops are roughly similar in size, ranging from 45–55 mm in length when mature, while pen shells can achieve lengths greater than 200 mm (data from this study). Here, we show that pea crabs occur more frequently in large pen-shell hosts than in 2 species of smaller hosts, and that crabs in pen-shell hosts are larger than crabs found in smaller bay scallops. Mussels, the third host in our study area, appeared to host pea crabs infrequently, and crabs resident in mussels were smaller than in any other host.

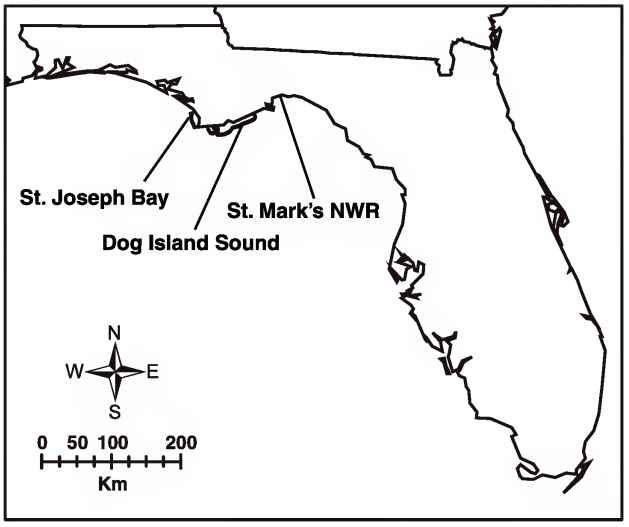

Figure 1. Collection sites in northwest Florida. Map Credit: The Florida Center for Instructional Technology, University of South Florida.

METHODS AND MATERIALS

During the summer of 2002, we collected the bivalves *Modiolus americanus*, *Argopecten irradians*, and *Atrina rigida* from 3 sites off the coast of northwest Florida (Figure 1): Dog Island Sound, immediately adjacent to the Florida State University Marine Laboratory; St. Mark's National Wildlife Refuge to the east; and St. Joseph Bay to the west.

We collected 100 mussels from St. Joseph Bay, 100 from St. Mark's NWR, and 93 from Dog Island Sound. Mussels were not abundant in Dog Island Sound, and we found only 93 individuals during the study period.

From St. Joseph Bay, we collected 50 pen shells, and 48 from St. Mark's NWR. We found no pen shells in Dog Island Sound during the study, despite extensive searches.

We also obtained 100 bay scallops each from Dog Island Sound and St. Mark's NWR. Weather conditions, principally hurricanes, and the short duration of this study precluded us from collecting bay scallops from St. Joseph Bay. All bivalves were collected by hand, using snorkel gear, in water up to 2 m deep.

We measured and recorded each bivalve's length (anterior/posterior), height (dorsal/ventral) and width (left/right valves) to the nearest 0.05 mm. We then opened every bivalve and examined it for the presence of pea crabs. If a crab was present, we recorded its sex and carapace width. When analysis at field sites was not practical, we transported the bivalves to the Florida State University Marine Lab in St. Teresa, Florida. At the lab, animals were maintained in seawater tables with constant water flow at a temperature of 25–28° C.

To compare mussel sizes from different sites, we executed a one-way analysis of variance using mussel length as the dependent variable and the collection site as the independent variable. Because we only had scallops from 2 sites, and pen shells from 2 sites, we compared bay scallop lengths from St. Mark's NWR and Dog Island Sound using a Student's *t*-test, and we compared pen-shell lengths from St. Mark's NWR and St. Joseph Bay using a separate Student's *t*-test.

To compare infestation rates within a host species between 2 collection sites, we used *G*-tests for independence (Sokal and Rohlf 1981). Additionally, we used Student's *t*-tests to compare carapace widths of pea crabs found in pen shells and pea crabs found in bay scallops. In one comparison (the comparison of pea crab carapace widths from pen shell and bay scallop hosts at St. Mark's NWR), the assumption of equal sample sizes was violated. Finally, among pea crabs found in a single host species, we sought relationships between pea crab carapace width and host size using linear regression analyses. We used bivalve length, height, and width as independent variables in separate regression analyses; pea crab carapace width was always used as the dependent variable.

RESULTS

Bivalve sizes, infestation rates, and pea crab sizes from different sites

Modiolus americanus. Mean length of collected mussels did not vary from site to site: mussels were 44.7 ± 6.8 mm (mean ± 1 standard deviation) in St. Joseph Bay; 45.4 ± 7.9 mm in Dog Island Sound, and 45.8 ± 10.6 mm in St. Mark's NWR. These values are not significantly different (ANOVA, $F = 0.415$, $P = 0.66$, df = 292).

Pea crabs rarely used mussels as a host. None of the 100 mussels collected from St. Joseph Bay contained pea crabs. One of the 100 mussels collected from St. Mark's NWR contained a small immature female pea crab with a carapace width of 5.5 mm. Similarly, one of the 93 mussels collected from Dog Island Sound also contained a female with a carapace width of 6.5 mm (Table 1).

Argopecten irradians. Bay scallops varied in size between the 2 collection sites. Scallops obtained from Dog Island Sound were significantly larger (longer in length) than those obtained from St. Mark's NWR (Student's *t*-test, $t = 16.798$, $P = 0.0001$, df = 196; Figure 2).

The infestation rate in bay scallop hosts was more than four times higher in St. Mark's NWR (Table 1). Only 4% of the bay scallops collected from Dog Island Sound contained pea crabs; all 4 of the crabs collected were female. In contrast, 17% of the bay scallops from St.

TABLE 1

Bivalves collected at each of 3 field sites and rates of infestation by the pea crab.

Bivalve	Location	*N*	Infected	% Infected
Modiolus americanus	St. Joseph Bay	100	0	0.0
Modiolus americanus	Dog Island Sound	93	1	1.1
Modiolus americanus	St. Mark's NWR	100	1	1.0
Argopecten irradians	Dog Island Sound	100	4	4.0
Argopecten irradians	St. Mark's NWR	100	17	17.0
Atrina rigida	St. Joseph Bay	48	33	68.8
Atrina rigida	St. Mark's NWR	50	37	74.0

Mark's NWR were infested; at this site, 13 (76.5%) of collected pea crabs were female, and 4 were male (23.5%). The difference between infestation rates at the 2 sites was significant (*G*-test for independence, $G = 9.381$, $P = 0.0022$, df = 1). All pea crabs occupying bay scallops were found living singly, irrespective of collection site.

Larger bay scallops in Dog Island Sound hosted larger pea crabs (Figure 2). The mean carapace width of female pea crabs found in bay scallops at St. Mark's NWR was 8.3 mm. The mean size of the female pea crabs found in bay scallops from Dog Island Sound was 9.5 mm. Because only 2 female pea crabs were found in the 100 bay scallops collected from Dog Island Sound, the mean carapace width was calculated using 2 additional female pea crabs found in other bay scallops from that site (G. Farley, unpublished data). The difference in mean female pea crab size from the 2 locations was not significant (Student's *t*-test, $t = 1.239$, $P = 0.2344$, df = 15). The mean size of the male pea crabs found in bay scallops at St. Mark's NWR was 5.7 mm.

Atrina rigida. Pen shells in St. Joseph Bay were significantly larger than pen shells from St. Mark's NWR, (Student's *t*-test, $t = 5.910$, $P = 0.001$, df = 96; Figure 3). Pen shells from the 2 sites were infested with pea crabs at a similar rate (*G*-test for independence, $G = 0.3244$, $P = 0.569$, df = 1). Pea crabs were found in 68.8% of pen shells from St. Joseph Bay, while 74.0% of pen shells from St. Mark's NWR were infested with pea crabs (Table 1). Most of the infested pen shells from both sites contained female pea crabs: 83.8% at St. Mark's NWR and 81.8% in St. Joseph Bay. Male-only infestation accounted for 16.2% of infested pen shells from St. Mark's NWR and 18.2 % of those infested from St. Joseph Bay.

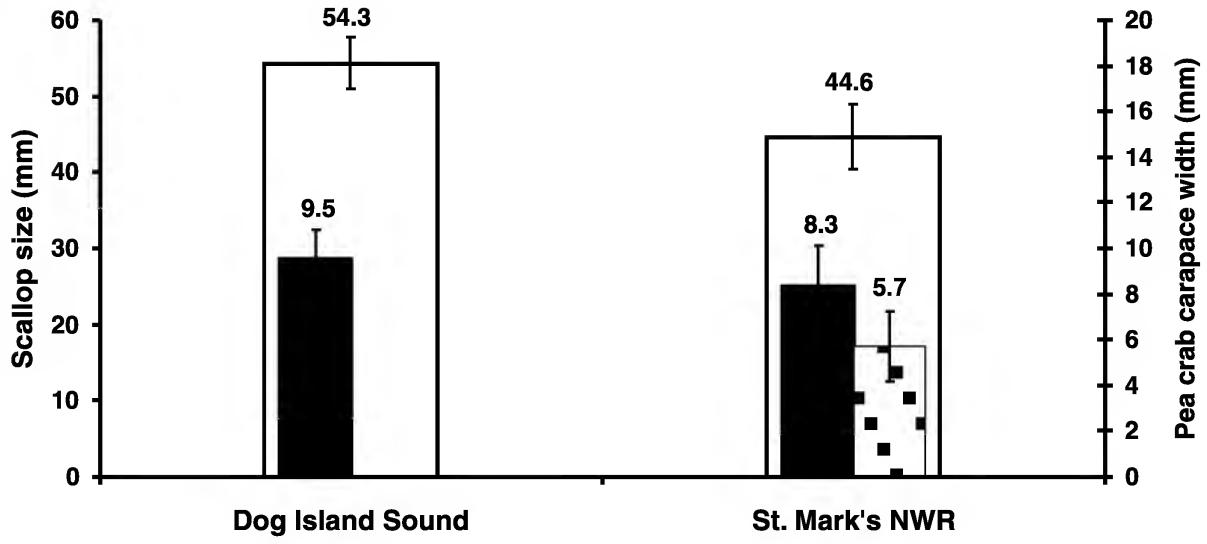

Figure 2. Mean lengths (mm, ± 1 SD) of bay scallops and mean carapace widths (mm, ± 1 SD) of male and female pea crabs at 2 sites. Large white bars are bay scallop lengths; small black bars are female pea crab carapace width; small striped bars are male pea crab carapace width. Bay scallops from Dog Island Sound were significantly larger than bay scallops from St. Mark's NWR. Female pea crabs were larger, although not significantly so, in bay scallops from Dog Island Sound; low numbers of crabs in Dog Island Sound may be obscuring a true difference in crab carapace widths.

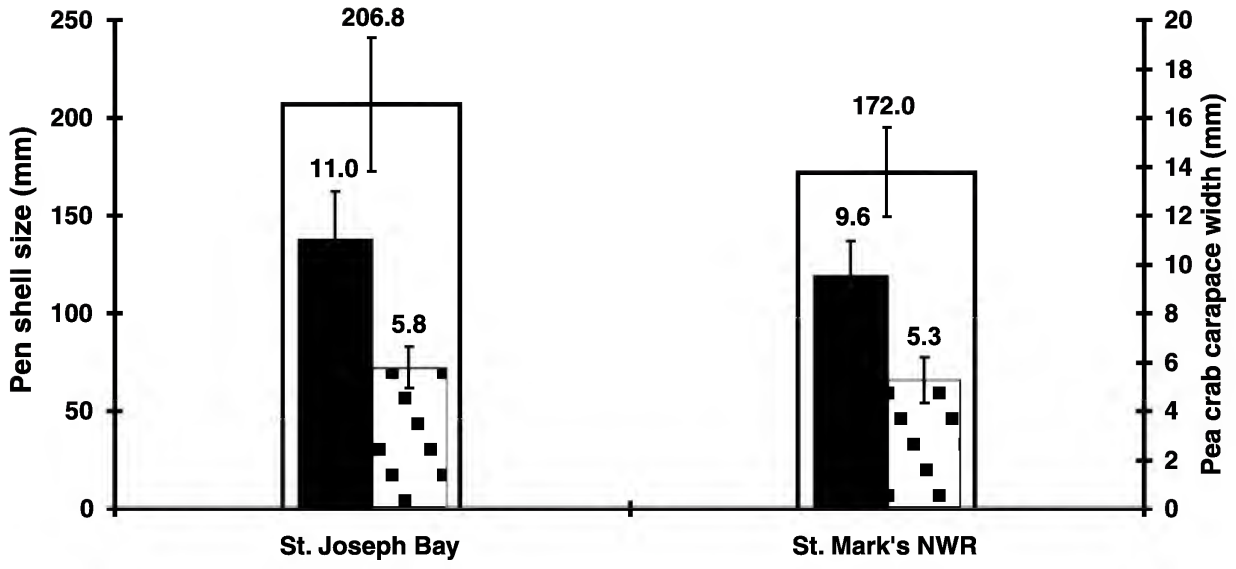

Figure 3. Mean lengths (mm, ± 1 SD) of pen shells and mean carapace widths (mm, ± 1 SD) of male and female pea crabs at 2 sites. Large white bars are pen shell lengths; small black bars are female pea crab carapace width; small striped bars are male pea crab carapace width. Pen shells from St. Joseph Bay were significantly larger than pen shells from St. Mark's NWR. Larger pen shells in St. Joseph Bay were host to larger female pea crabs, but male crabs were similar in size in all pen shell hosts.

Larger pen shells in St. Joseph Bay were hosts to significantly larger female pea crabs (Student's *t*-test, $t = 3.188$, $P = 0.0023$, df = 56; Figure 3). Mean carapace width for female pea crabs from St. Joseph Bay pen shells was 11.0 mm. At St. Mark's NWR, the mean carapace width of female pea crabs was 9.6 mm.

Male pea crabs from pen shell hosts were similar in size at both sites (Figure 3). Mean carapace width among male pea crabs at St. Joseph Bay was 5.8 mm, and pea crabs averaged 5.3 mm carapace width at St. Mark's NWR. This was not a significant difference (Student's *t*-test, $t = 2.064$, $P = 0.7388$, df = 24).

Pen shells were the only host in this study to harbor more than one pea crab per bivalve. Most multiple infestations consisted of one female pea crab and at least one male. Of pen shells containing female pea crabs, 14.8 % (4 of 48) from St. Joseph Bay and 8.1% (3 of 50) from St. Mark's NWR also contained one male. One pen shell from St. Joseph Bay contained 2 males. One pen shell at St. Mark's NWR contained a female and 2 males, and one pen shell from St. Joseph Bay contained one female and 3 male pea crabs.

Smaller pen shells had higher infestation rates. When pen shells from both collection sites were pooled, the percentage of pen shells hosting pea crabs declined with increasing host size (Figure 4). This pattern was not evident among scallop hosts.

Pea crabs were larger in a larger host bivalve. The only site at which we found both large and small host bivalves in abundance was St. Mark's NWR. At this site, larger bivalves, pen shells, hosted larger female pea crabs than bay scallops (Figure 5). The mean carapace width of female pea crabs found in pen shells was 9.6 mm ($n = 31$), whereas the mean carapace width of females found in scallops was 8.3 mm ($n = 13$). This was a significant difference (Student's *t*-test, $t = 2.470$, $P = 0.0177$, df = 42), although the assumption of equal sample sizes has been violated in this test.

For male pea crabs, this trend was not significant. Mean carapace width of male pea crabs living in pen shells was 5.3 mm ($n = 11$), which did not differ significantly from the mean carapace width of those found in scallops, 5.7 mm ($n = 4$) (Student's *t*-test, $t = 0.699$, $P = 0.497$, df = 13). Again, the assumption of equal sample sizes is violated in this test.

Female pea crab size was not strongly correlated with bivalve size within a host species. There was a notable correspondence between the larger host species and larger size of female pea crabs. However, even though this trend was significant between the different bivalves, relationships between host size and pea crab size within host species are weak for pen shell hosts. Variation in pen shell length, the shell dimension with the greatest explanatory power of any we measured, explains only 9.5% of the variation in pea crab carapace width using linear regression ($r^2 = 0.095$, $P = 0.019$; Figure 5).

All other linear regression analyses, including regressions of pea crab carapace size on pen shell width and

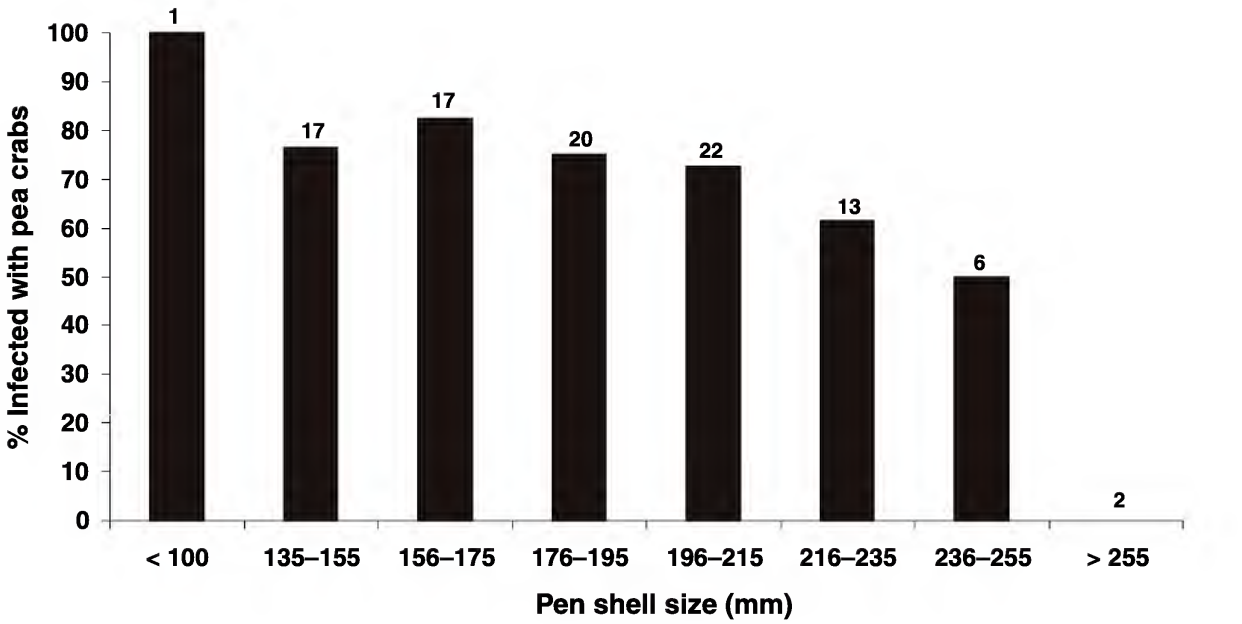

Figure 4. The proportion of pen shells infested with pea crabs, as a function of pen shell length. Data have been pooled from both collection sites, and the number above each bar indicates the number of pen shells in that grouping. Smaller pen shells host greater numbers of pea crabs.

height, were not significant. Linear-regression relationships between pea crab carapace width and scallop length, width, and height were all nonsignificant, although a regression of pea crab carapace width against scallop length did show a positive slope.

DISCUSSION

Mussels from the 3 different geographic areas we sampled did not host pea crabs very frequently. Out of 300 mussels collected, only 2 pea crabs were found; both pea crabs were small females. However, this may be a limitation of our one-time study, and not an accurate reflection of the biology of pea crabs. In casual observations of mussels from Dog Island Sound prior to the study, we found an infestation rate of about 10%. Pearce (1969) and Campos (1989) state that individual pea crabs use multiple hosts at different stages in their life history, and Bierbaum and Ferson (1986) found that small (< 6 mm), immature females are able to move from host to host. Kruczynski (1974) found that another species of mussel, *M. edulis*, was more likely to be infested with pea crabs in deeper water than we surveyed (> 10 ft in his study). A study of greater duration than ours, and covering a greater depth range than ours, is needed to fully investigate the relationship between mussels and pea crabs in the northern Gulf of Mexico.

Bay scallops hosted fewer pea crabs than pen shells. The percentage of scallops hosting pea crabs varied strongly among collection sites, from 4% in Dog Island Sound to 17% at St. Mark's NWR. This may reflect differences in larval recruitment of pea crabs to hosts between the 2 sites, a hypothesis that our data do not address. Alternatively, because scallops in Dog Island Sound were larger than scallops at St. Mark's NWR, it remains possible that larger scallops are able to resist infestation by pea crabs. However, bivalve anatomy offers no ready mechanism for resistance, and to the best of our knowledge, no such resistance has been reported in the literature.

Pen shells were frequent hosts of pea crabs, regardless of collection site: about 70% of pen shells collected were host to at least one pea crab. Pen shells are large, sessile bivalves that can not draw their valves together tightly; even when its adductor muscles are contracted, there is a gap between the shells as they protrude from the sea bed. This unique facet of pen-shell anatomy may make them vulnerable to infestation by symbionts, although in our survey, the only endosymbiont we ever encountered in pen shells was the pea crab. While the outsides of pen shells are heavily fouled by a wide variety of invertebrates, we found only pea crabs inside the mantle cavities. This suggests that pen shells tolerate pea crabs, or that pea crabs defend their hosts against other invading species. However, to date, no studies have explored either of these hypotheses.

It is not clear why there was such a large difference in the infestation rates of 2 common hosts. Pea crabs may show a preference for a certain host, but the literature is contradictory on this point. Derby and Atema (1980) test-

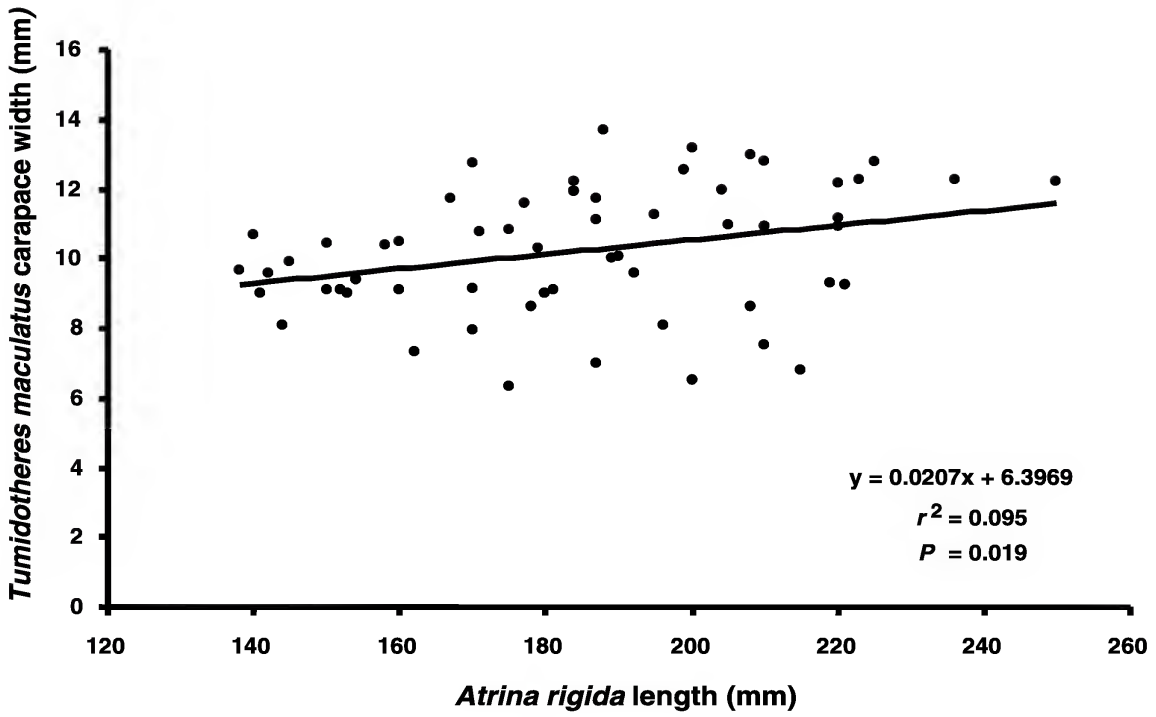

Figure 5. Pea crab carapace width (mm) as a function of pen shell length (mm). A weak but significant trend indicates that larger pen shells host larger pea crabs.

ed pea crabs taken from mussels, *M. edulis*, for attraction to 4 different bivalves and found that pea crabs exhibited a strong preference for *M. edulis*. However, Sastry and Menzel (1962), working in the same region that we studied, performed host recognition experiments with pea crabs taken from bay scallops; in their experiment, pea crabs showed no preference for scallops over pen shells. Whether the pea crab discriminates among host species remains unresolved.

Pen shells may harbor more pea crabs than scallops because pen shells are a year-round occupant of seagrass beds in northern Florida. Bay scallops are mobile, and populations in shallow seagrass beds wane in the winter months. Pen shells, by contrast, are infaunal, and can be found year-round at our study sites (pers. obs.). Stationary, persistent shelters might gradually accumulate pea crabs over time, so it is possible that the long-term persistence of pen shells contributes to the larger numbers of endosymbionts we found. However, our data show that smaller, presumably younger pen shells have higher endosymbiont loads, and extremely large pen shells—those greater than 255 mm in length—have the fewest endosymbionts of any size class. Therefore, our data appear to contradict the hypothesis that older, stationary pen shells may gradually accrue more endosymbiotic pea crabs.

The only host bivalves that ever housed multiple pea crabs in our study were pen shells, the largest host species we collected. While one of us (GSF) has seen photographs, taken in the lab, of multiple pea crabs in a single bay scallop, we never found this condition in the field. Infestations involving multiple pea crabs were rare during our study period, occuring in only 10 of 200 hosts, and all multiple infestations except one were single-female, multiple-male assemblages. The single exception was a pen shell that hosted 2 male pea crabs.

Data from other crab species (Beck 1995, Kuhlmann and Walker 1999) led us to expect that larger host bivalves should hold larger pea crabs. Our data support that hypothesis: at St. Mark's NWR, female crabs living in pen shells were significantly larger than female pea crabs living in scallops. The same trend is apparent within host bivalve species; larger pen shells in St. Joseph Bay hosted significantly larger pea crabs than the smaller pen shells in St. Mark's NWR. Likewise, pea crabs living in larger bay scallops in Dog Island Sound were larger than pea crabs living in smaller bay scallops in St. Mark's NWR, although small numbers of pea crabs in Dog Island Sound preclude adequate statistical support for this trend. Our data, taken as a whole, indicate that the pea crab, a symbiotic pinnotherid crab, conforms to patterns found in free-living xanthid crabs (Beck 1995, Kuhlmann and Walker 1999). Growth in shelter-dwelling brachyuran crabs seems limited by shelter size, whether shelter is biotic or abiotic.

Data from male pea crabs supports this conclusion, albeit in a roundabout fashion. Male pea crabs were strikingly uniform in size in our study, regardless of host species, host size, or collection site. One possible explanation for this trend is that dwarf male pea crabs have terminal growth and reach a well-defined size at maturity that is consistent across populations. Alternatively, male pea crabs may all reach a similar size because male pea crabs move from host to host, and do not rely on host organisms for food (Sastry and Menzel 1962, Bierbaum and Ferson 1986). Crabs that do not spend long periods in a single shelter may not be constrained in their growth. Further data from free-living crab species, such as portunid swimming crabs, is needed to test this hypothesis.

It is possible that we have documented not simply a difference in host size, but also a difference in host quality that could drive differences in pea crab size and frequency among hosts. In pen shell hosts, pea crabs occur more frequently, attain larger sizes, and more often occur in groups. Because pea crabs feed on the gills of bivalve hosts (Bierbaum and Ferson 1986, Bierbaum and Shumway 1988), it is possible that the larger size of pen shells provides pea crabs with more gill surface area and therefore more food than the smaller gills of smaller bivalve hosts. Our data do not address this hypothesis directly, and this hypothesis does not exclude the possibility that shelter size also contributes to pea crab size and frequency.

The possibility that the pea crab uses multiple hosts at different life-history stages (Pearce 1964, Campos 1989) also confounds our conclusions. Whether more mature pea crabs prefer pen shell hosts, specifically, or whether the pea crab chooses among hosts, is unclear in the literature. However, it seems likely that life history, along with host quality and host size, contributes to the patterns we witnessed.

ACKNOWLEDGMENTS

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Comparison of Fish Assemblages and Water Quality in Two Marinas in the British Virgin Islands

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SHORT COMMUNICATION

COMPARISON OF FISH ASSEMBLAGES AND WATER QUALITY IN TWO MARINAS IN THE BRITISH VIRGIN ISLANDS

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Introduction

Eutrophication is a widespread problem in tropical marine environments that leads to the increase of nutrients in a water body, usually nitrate and phosphate, and is usually associated with the discharge of untreated sewage, intensive farming or fertilizer-enriched agricultural runoff (Wu 1999). Common symptoms are increased N and P levels, increased macroalgal production in shallow areas, reduced dissolved oxygen, loss of seagrass and coral habitats and changes in the fish community (Hallock and Schlager 1986, Granelli et al. 1990, Valiela 1995, Hemminga and Duarte 2000). Direct chemical testing to establish pollution levels can be difficult because of sharp pollution gradients, rapid dilution effects, changing tides and currents, variable pollutant concentrations, varying pollution activities, unavailability of water quality test kits, a prohibitive range of pollutants to test for and high testing costs (Resh et al. 1995). Many of these problems can be countered with bioassessment methods that use biotic indicators to assess ecosystem integrity (Karr 1981, Noss 1990, Wright et al. 1993, Chessman 1995). Biotic indicators of pollution have several advantages over chemical methods: they are broad-ranged, detect many forms of pollution, reflect pollution history and indicate overall health of the system.

Animal bioindicators should be: 1) sufficiently sensitive to disturbance, 2) widely distributed, 3) capable of living in a wide range of conditions, 4) relatively independent of sample size, 5) easy and cost effective to study, 6) able to differentiate between natural and man-made disturbance, and 7) relevant to ecologically significant phenomena (Noss 1990). Fish meet many of these criteria and have been included in several freshwater bioassessment protocols, sometimes referred to as biological integrity indices (Larkin and Northcote 1969, Karr 1981, Karr 1990, Hughes et al. 1998). Marine fish have been widely used as indicators of coral cover and overfishing (Bell and Galzin 1984, Findley and Findley 1985, Roberts 1995, Russ and Alcala 1998), but few studies have successfully used marine fish assemblages as indicators of pollution. One reason is that it is difficult to determine the direct effects of pollution on marine fish assemblages because natural experiments are usually confounded by habitat alteration due to dredging, siltation and pollution. This study aims to assess the potential of marine fishes as bioindicators using artificial reefs as habitat controls in 2 marinas with different pollution levels.

Materials and Methods

The study was carried out in 2 marinas with high volumes of charter yacht traffic on the west end of Tortola, in the British Virgin Islands (Figure 1). Nanny Cay has berths for 180 yachts. It is a shallow bay with 2 small channels to allow water flow through the quiet backwaters of the bay, but the amount of clean water entering the bay is limited and depends on tide and prevailing currents. The bay is lined with mangroves on one side, and the substrate consists of mud covered in macroalgae but becomes sandier towards the mouth of the bay. Housing and shopping complexes line either side of the bay, and at least one bank-side housing complex discharges wastewater directly into the bay. Soper's Hole has 150 berths and is comparable in size to Nanny Cay; it is lined with mangroves on one side (Figure 1) and has a sandy substrate with some muddy areas. Sparse patches of macroalgae and seagrass dot the marina, and a deep channel between the island and the mainland allows water to flow through the bay. Several shopping complexes and housing developments line the bay, but there are no visible land-based wastewater discharges.

Ten artificial reefs were built in each bay, ranging from the more sheltered backwaters to the mouth of the bay. Rocks between 10 and 20 cm diameter were gathered from the shoreline and arranged on the substrate to form a 1m x 1m square mound, about 40 cm high. These were left for one week prior to monitoring.

Stations were visited once every week for 3 weeks in August 2002. All fish on or within 30 cm of the reef were identified and counted during a 5-minute observation period. Depth (m) was measured using a fibreglass measuring tape, and temperature (^{o}C) was measured using a waterproof digital thermometer. Water clarity (m) was measured using a secchi disc attached to a measuring tape. One person held the disc about 30 cm below the water surface,

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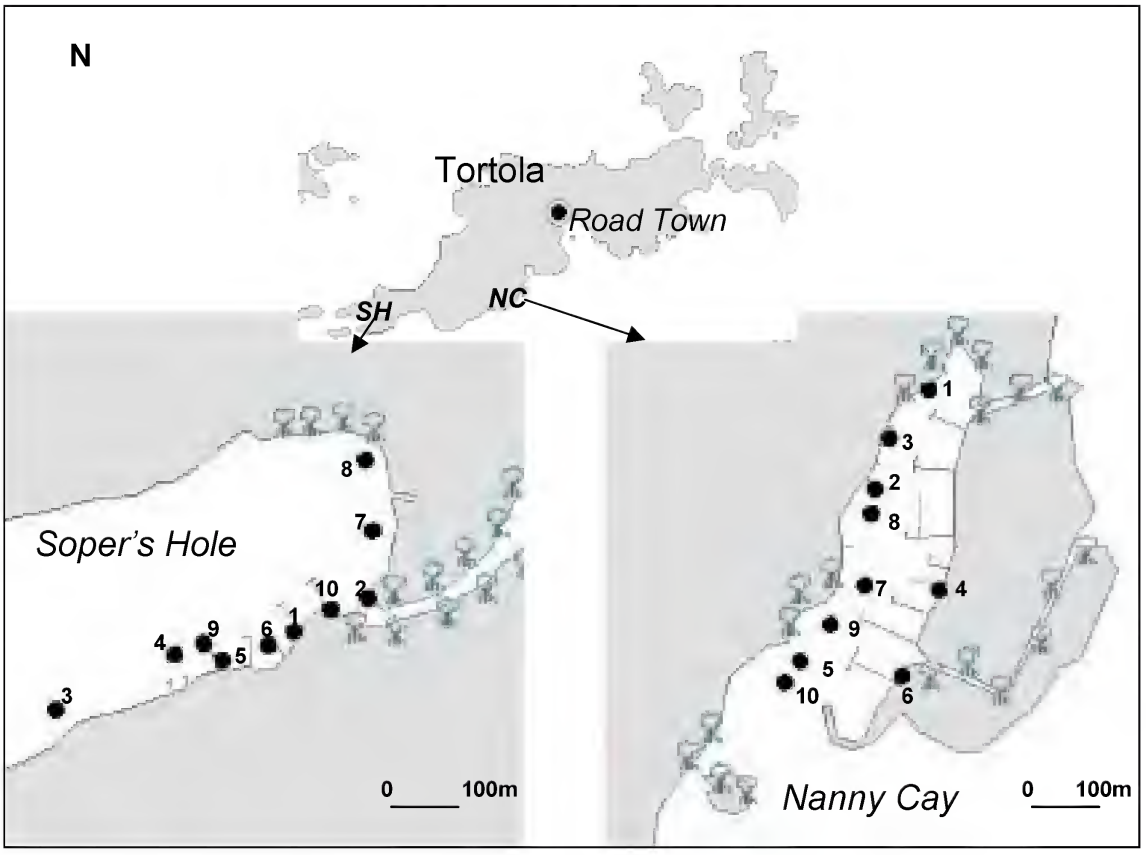

Figure 1. The location of twenty artificial reefs in the 2 marinas Nanny Cay (NC) and Soper's Hole (SH) on Tortola, an island between the Atlantic Ocean and the Caribbean Sea, west of Puerto Rico.

while the other swam away from the disc with the tape, measuring the distance at which the disc was no longer visible. Phosphate (mgl^{-1}) and nitrate (mgl^{-1}) concentrations were measured using low-range reagents and a Hach DR 850 photo spectrometer. Dissolved oxygen (DO) levels (mgl^{-1}) were measured within the first hour after sunrise each day, before oxygen levels increased due to photosynthesis, using a portable HANNA H1-9142 dissolved oxygen meter.

Differences between the mean number of fish, species richness, Shannon-Weiner diversity, depth, water clarity, DO, phosphate, and nitrate in each bay were tested using a two-sample t test; significant P values were calculated using the Bonferroni correction for multiple comparisons, dividing the standard critical $P = 0.05$ by the number of related measurements ($n = 8$)(Bonferroni 1935).

RESULTS

Nanny Cay displayed some characteristic symptoms of eutrophication: low visibility, high phosphate, and nitrate concentrations and low DO levels (Figure 2). While the absolute figures are not exceptional by global standards, they were significantly different from Soper's Hole, which was comparatively unpolluted and had higher fish species richness and abundance than Nanny Cay. The community differentiation table shows that 24 species were unique to Soper's Hole, while only 4 species were unique to Nanny Cay (Table 1).

At both stations there are water quality gradients with some stations having poorer water quality and others having better water quality (Figure 2a–h). A multiple regression model using the measured physicochemical water quality variables (but excluding visibility because of multicolinearity problems) accounted for 48% of the observed variation in fish species richness but did not explain a significant proportion of the variation in fish abundance (Table 2). In the multiple regression model, nitrate concentration was the best predictor of fish species richness, followed by phosphate concentration (Table 2).

DISCUSSION

The 2 marinas had quite distinctive fish assemblages and water quality, and these initial results indicate that fish assemblages on artificial reefs have a strong potential for

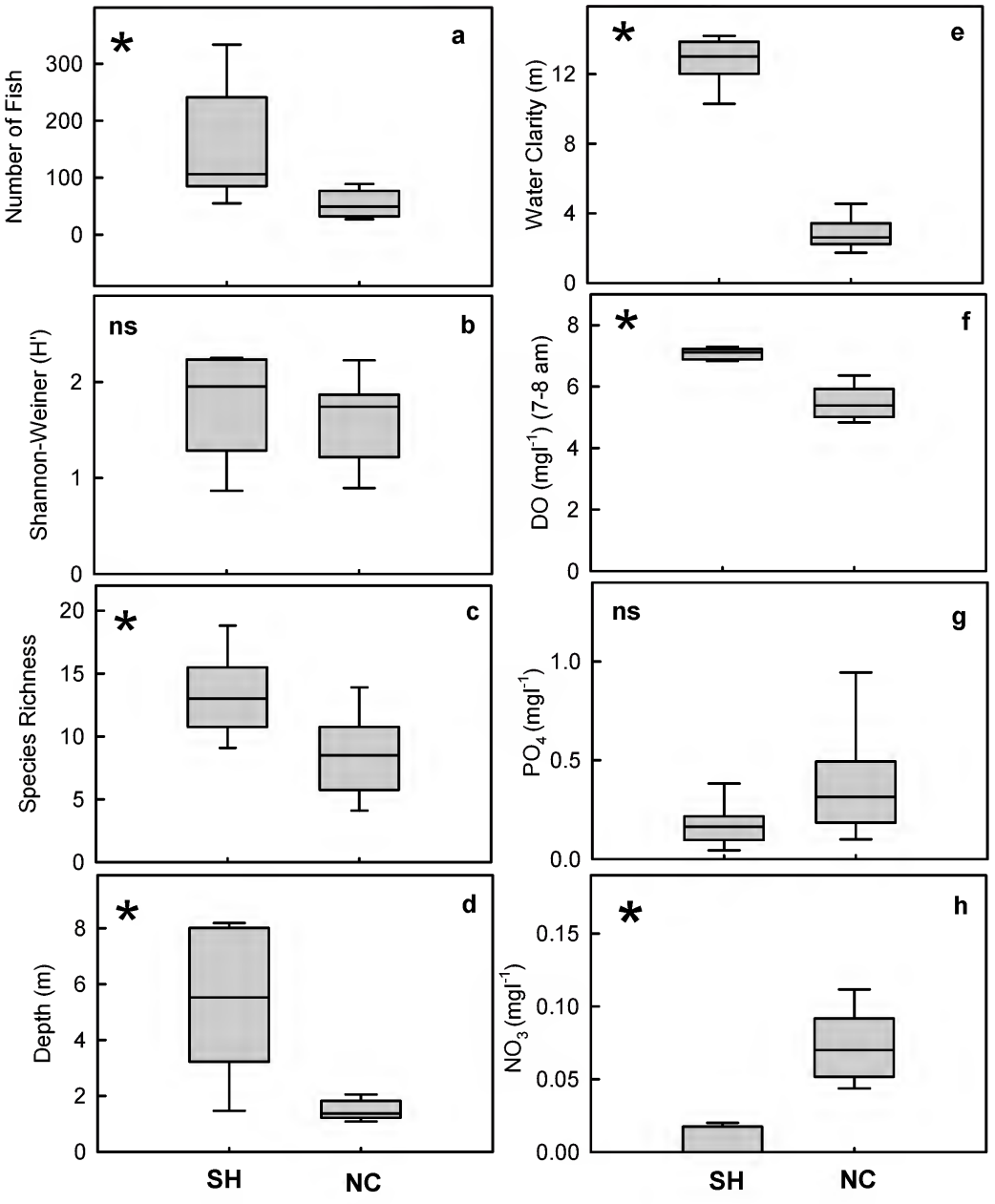

Figure 2. Boxplots illustrating the variation in biological and physicochemical variables in Nanny Cay (NC) and Soper's Hole (SH). Differences between the means were tested using a two-sample t test. * = significant difference at Bonferroni corrected *P* = 0.00625 corrected critical value.

use as biotic indicators of marine pollution. However, poor water quality is one of many factors that may have been responsible for the observed differences. For example, it is well established that proximity to other habitats, direction and strength of prevailing currents, and depth are known to affect local patterns of fish species richness and abundance (Yanez et al. 1993, Ody and Harmelin 1994, Nagelkerken et al. 2000). Because these factors were not considered, this study lacks a true control. This is a recurring problem in many environmental impact studies. One way to counter this problem is to sample a wide range of different sites, with many polluted and many unpolluted situations throughout the region to establish a wide range of validity (Wright et al. 1993). Next these data should be analysed to determine whether a typical or 'reference' state can be established which takes variation due to natural factors into account, but that can serve as valid comparisons for truly impaired stations (Wright et al. 1993, Chutter 1998).

Although such a broad survey was beyond the scope of this initial study, the gradient analysis (multiple regres-

TABLE 1

Community differentiation table of species counted on the 3 sampling occasions at Soper's Hole (SH) and Nanny Cay (NC) stations. Symbols refer to the mean abundance of that species on a logarithmic scale: · ≤ 1, • = 1–10, ● = 10–100. The order of species in the species list was determined using a TWINSPAN analysis of species (Hill 1979).

	SH1	SH2	SH3	SH4	SH5	SH6	SH7	SH8	SH9	SH10	NC1	NC2	NC3	NC4	NC5	NC6	NC7	NC8	NC9	NC10
Bothus lunatus								·												
Coryphopterus personatus								·												
Haemulon aurolineatum					●		•	•	·											
Stegastes planifrons						·														
Sphoeroides spengleri							·													
Stegastes variabilis						·														
Scarus vetula						·														
Acanthurus chirurgus									·											
Acanthurus coeruleus	•			·					·											
Calamus calamus	·									·										
Coryphopterus glaucofraenum	•	·	·	•	•	•		•	•	•										
Canthigaster rostrata	·																			
Caranx ruber				·	•	·		·	·	•										
Gerres cinereus	·																			
Hypoplectrus chlorurus									·											
Mulloidichthys martinicus									•	·										
Pseudupeneus maculatus	•				·				·	•										
Sparisoma aurofrenatum	•			·	•	·	·	•	·											
Sparisoma viride	·																			
Thalassoma bifasciatum				·																
Apogon binotatus			·																	
Clepticus parrae			·																	
Hypoplectrus puella	·	·	·	·					·	·										
Pomacanthus paru			·																	
Acanthurus bahianus	·		•	•	·	•		•	•	•	•		·		•	·				
Lutjanus synagris	•	•	●		·	●	•	•	·	•		·		·			·		·	•
Sparisoma radians		•				·	·		·	·						·				
Chaetodon capistratus	·			·		•	•		•	•		•	•	•	•	·	·			
Halichoeres bivittatus	•	•		•	•	•	•	·	•	•	·			·	·	·	·			·
Ocyurus chrysurus	•	•	●	•	•	•	•	•	•	•	·		·	•		·	·	·	•	·
Scarus iseri/taeniopterus	•	•				•	•	•	·		•		•		•	•	•	•		●
Stegastes leucostictus	·	·			·	·		·	·				·	·	•	•	·	•		
Haemulon flavolineatum		·			•		●	•	·		•	·	•	•	•	•	•		•	·
Lutjanus griseus						·		·			·	•	·	·		•		•	•	
Stegastes dorsopunicans																			·	
Sphaeroides testudineus		·					·				·									
Eucinostomus spp.		•								•	•		·	·		•	•	•	•	
Haemulon plumieri	·	·	•								·				·	•				
Abudefduf saxatilis															·					
Caranx latus																·				
Gymnothorax funebris											·							·		
Halichoeres poeyi											·									
Haemulon sciurus											•									
Lutjanus apodus											·		·		·	·	•			
Lophogobius cyprinoides													·							
Lactophrys triqueter															·					
Malacoctenus macropus		·														·		·		

TABLE 2

Multiple regression models of total number of species and total abundance of fishes observed on experimental reefs. (a) Predictor variables include nitrate, phosphate, dissolved oxygen and depth. Examination of the standardized beta coefficients revealed that only nitrate: $B = -0.58$, $t = -2.27$, $P = 0.04$* and phosphate: $B = -0.40$, $t = 2.18$, $P = 0.04$* were significant predictors of fish species richness.

		Sum of squares	df	F	Sig.	Adj. r^2
Species richness	Regression	172.655	4	5.434	.007(a)	0.48**
	Residual	119.145	15			
	Total	291.800	19			
Abundance	Regression	110.378	4	2.800	.064(a)	0.27ns
	Residual	147.809	15			
	Total	258.187	19			

sion) provides suitable statistical evidence supporting the hypothesis that fish species richness on artificial habitats is indeed related to water quality, making fishes assemblages potentially useful bioindicators. The artificial reefs in the most polluted areas had the lowest fish species richness and abundance, as might be expected from a strongly eutrophic system (Deegan et al. 2002).

Because nutrients are often a factor limiting primary production in aquatic environments, increasing the nutrient budget of aquatic systems through mild eutrophication can lead to an increase in overall algal productivity that may cascade up the food chain and cause an increase in fish productivity (Larkin and Northcote 1969, Hulot et al. 2000). In severely eutrophic systems, however, the decay of nutrient-rich pollutants creates a very high biological oxygen demand leading to diel fluctuations in DO and elevated carbon dioxide levels that may make fish avoid heavily eutrophied zones (Larkin and Northcote 1969). The adverse effects of other chemicals also associated with severe eutrophication, such as ammonia, may adversely affect fish and deter them from strongly eutrophic areas. As fish respond to a wide range of water quality variables, they will be useful indicator taxa in eutrophication studies (Larkin and Northcote 1969).

TABLE 3

Mean characteristics of coastal marine waters of different trophic states from Häkanson (1994).

	Nitrate (mgl^{-1})	Phosphate (mgl^{-1})
Oligotrophic	< 0.26	< 0.01
Mesotrophic	0.26–0.35	0.01–0.03
Eutrophic	0.35–0.40	0.03–0.04
Hypertrophic	0.40+	0.04+

Nitrates were not excessively concentrated in either bay, although Nanny Cay had the highest levels, the range in NO_3 concentration of 0–0.1 mg l^{-1} was well below the 0.26 mg l^{-1} threshold described by Häkanson (1994), and both bays would hence be classified as oligotrophic, assuming there were no excessive phosphate concentrations. However, the phosphate levels in Nanny Cay ranged mostly between 0.02 and 0.09 mg l^{-1} and include the wide spectrum of marine classifications ranging from mesotrophic to hypertrophic, but mostly eutrophic (Figure 2, Table 3). Soper's Hole, however, would be classified as mostly oligotrophic or mesotrophic (Figure 2, Table 3). Other workers in the Caribbean have noted that phosphate concentrations of 0.0103–0.0111 mgl^{-1} (mesotrophic) had adverse effects on corals (Tomascik 1991).

There was a distinct gradient in fish species richness associated with the pollution gradients, with more polluted stations having fewer species, but not all species were detrimentally affected by poor water quality. In fact, mojarras apparently increased in abundance in more polluted areas, a pattern that has been noted elsewhere Gratwicke (2004). Other examples of apparently 'tolerant' fish include *Lutjanus griseus* and *Lutjanus apodus*. These 'tolerant' fish are all mangrove-associated (Chaves and Otto 1999, Nagelkerken et al. 2002) and might therefore be pre-adapted to low dissolved oxygen conditions associated with decomposing mangrove detritus. Other species are probably more sensitive to pollution and an advanced biomonitoring index might weight the presence or absence of each species according to its apparent pollution tolerance.

In conclusion, we believe that this study has 2 main achievements. First, using very inexpensive artificial reefs as habitat controls when investigating the effects of water quality on fishes in aquatic environments is an appropriate method. Second, a gradient analysis showing that 2 water

quality variables were significantly related to fish species richness found on the reefs means that this method deserves more widespread testing to extend the range of validity of these results.

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Marionia tedi Ev. Marcus, 1983 (Nudibranchia, Tritoniidae) in the Gulf of Mexico: First Record of an Opisthobranch Mollusk from Hydrocarbon Cold Seeps

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SHORT COMMUNICATION

MARIONIA TEDI EV. MARCUS, 1983 (NUDIBRANCHIA, TRITONIIDAE) IN THE GULF OF MEXICO: FIRST RECORD OF AN OPISTHOBRANCH MOLLUSK FROM HYDROCARBON COLD SEEPS

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Introduction

Cold seeps in the Gulf of Mexico contain relatively diverse molluscan assemblages primarily composed of species that support chemoautotrophic symbionts, such as vesicomyid and mytilid bivalves, but also numerous species of shelled gastropods, bivalves, monoplacophorans, and polyplacophorans (Cordes 2004).

Recent exploration of hydrocarbon seep sites in the Mississippi Canyon and the Vioska Knoll revealed the presence of an unidentified species of nudibranch. The present paper describes the single specimen collected, which constitutes the first published record of an opisthobranch mollusk from a cold seep. The material examined is deposited at the Field Museum of Natural History (FMNH).

Species Description

Marionia tedi Ev. Marcus, 1983
(Figures 1–3)

Marionia tedi Marcus 1983: 203–207, Figures 48–74.

Material examined

R/V *Seward Johnson II*, Submersible *Johnson Sea-Link* Dive 4605, Mississippi Canyon site 885 (28°03.903'N, 89°42.721'W), Louisiana Slope, USA, 1 specimen 16 mm preserved length, 15 September 2003, 624 m depth, leg. J. Voight (FMNH 306187).

R/V *Seward Johnson II*, Submersible *Johnson Sea-Link* Dive 3355, Viosca Knoll site 826 (29°09.3'N, 88°01.4'W), Louisiana Slope, USA, 540 m depth, photo only.

External morphology

Two specimens were photographed alive (Figure 1) and never collected. A single specimen was collected and here studied (FMNH 306187). The specimens are elongate in the living state, wider anteriorly. The dorsum bears a series of short and ramified dorso-lateral cerata, arranged in a single row (Figures 1–2). There are 12–16 cerata on each side of the body. The velum is bilobed with about 6 processes on each lobe. The rhinophores have 9 irregular, vertical lamellae and an elongate, ramified apex.

The color is uniformly translucent white with a pinkish tinge. The viscera are visible through the skin as an opaque white mass. Rhinophores, cerata and velum are the same color as the rest of the body.

Anatomy

Digestive system. The large, oval, muscular buccal bulb has a thick muscular ring near the anterior end, attach-

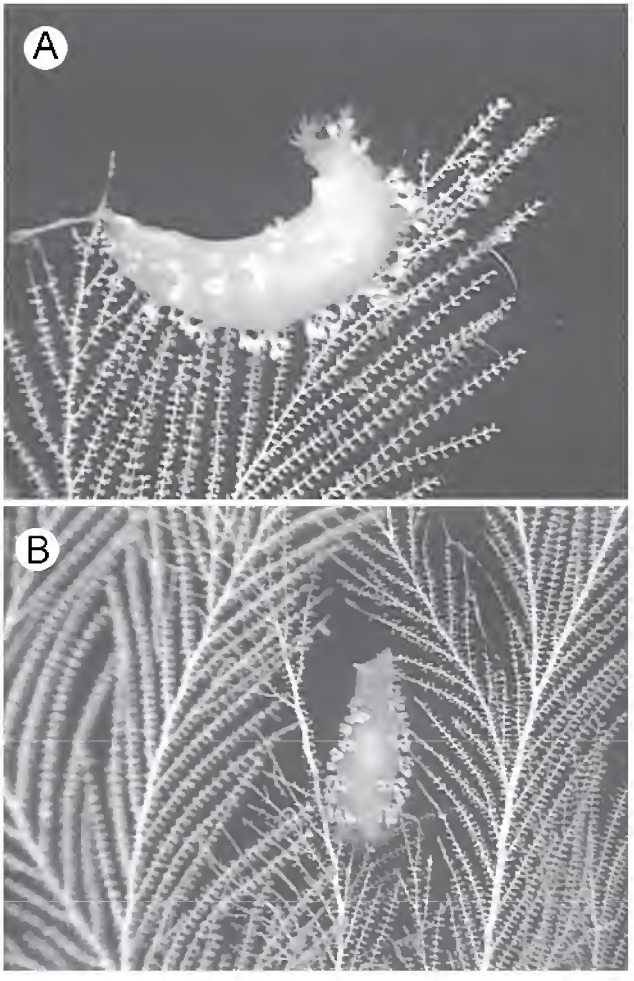

Figure 1. *Marionia tedi* Ev. Marcus, 1983 living animals on *Callogorgia americana* Cairns and Bayer, 2002. A, Animal from Mississippi Canyon (28°03.903'N, 89°42.721'W). B, Animal from Viosca Knoll (29°09.3'N, 88°01.4'W), photo by Stephane Hourdez.

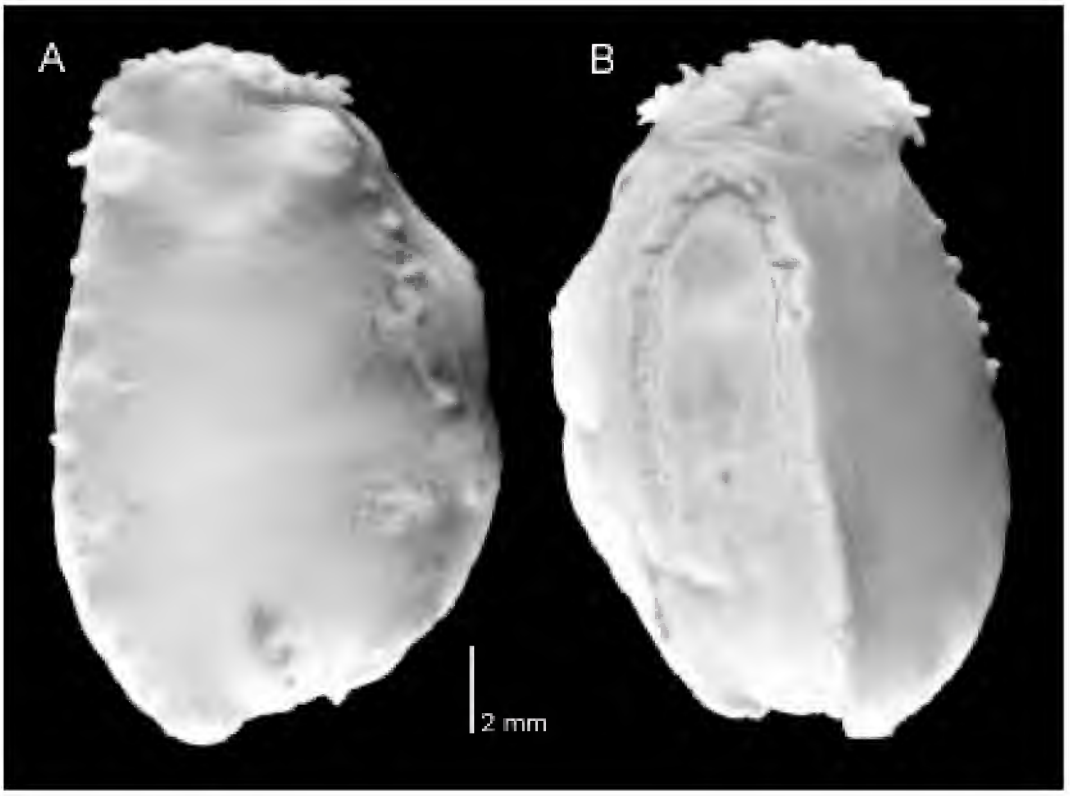

Figure 2. *Marionia tedi* Ev. Marcus, 1983, preserved specimen from Mississippi Canyon (FMNH 306187). A, Dorsal view. B, Ventral view.

ing to the body wall. Two long salivary glands connect with the buccal bulb on either side of the esophageal junction (Figure 3A). The esophagus is initially thin; it emerges from the dorsal end of the buccal bulb and runs towards the left side of the body. Right after passing through the central nervous system ring, it expands into a wider tube that connects to the digestive gland ventrally (Figure 3A). The stomach is oval, partially embedded in the digestive gland (Figure 3A) and contains numerous irregular, fragile, chitinous plates. At its distal end, the stomach connects to the intestine. The intestine is short and straight, running towards the right side of the body where it opens into the anus.

The jaws consist of 2 oval plates with an elongate masticatory border on each one (Figure 4D). The masticatory border contains numerous irregular rodlets (Figure 4E). The radular formula is 41 x 43.1.43 in the single 16-mm long examined specimen (FMNH 306187). The rachidian teeth are wide, with a strong triangular central cusp bearing a couple of minute denticles on each side (Figure 4A). On each side of the cusp there are 1–2 large, blunt denticles oriented towards the central cusp. The upper end of the rachian teeth have a conspicuous depression. The lateral teeth are hook-shaped and smooth, lacking denticles (Figure 4B). The cusp is normally short and blunt. The outermost teeth are smooth and elongate, with a sharp, triangular cusp (Figure 4C).

Reproductive system. The ampulla is elongate and small, with the hermaphrodite duct and the gonoduct opening on opposite ends (Figure 3E). The gonoduct is very short and connects directly into the female glands. The prostate is tubular, very long, folded and granular. It connects directly to the large and strongly muscular deferent duct (Figure 3C). The deferent duct opens into a common atrium with the vagina. The penis is elongate with a blunt apex bearing a central protuberance (Figure 3D). The vagina is long and curved. Near its proximal end it joins the irregular bursa copulatrix.

Central nervous system. The cerebral and pleural ganglia are fused together and are distinct from the pedal ganglion (Figure 3B). There are 2 and 3 cerebral nerves leading from the left and right cerebral ganglia respectively, one rhinophoral nerve leading from each cerebral ganglion, and one pleural nerve leading from each pleural ganglion. The buccal ganglia are near the rest of the central nervous system, joined to the cerebral ganglia by 2 relatively short connectives. The optical ganglia connect to long nerves leading to the eyes, which are situated at the

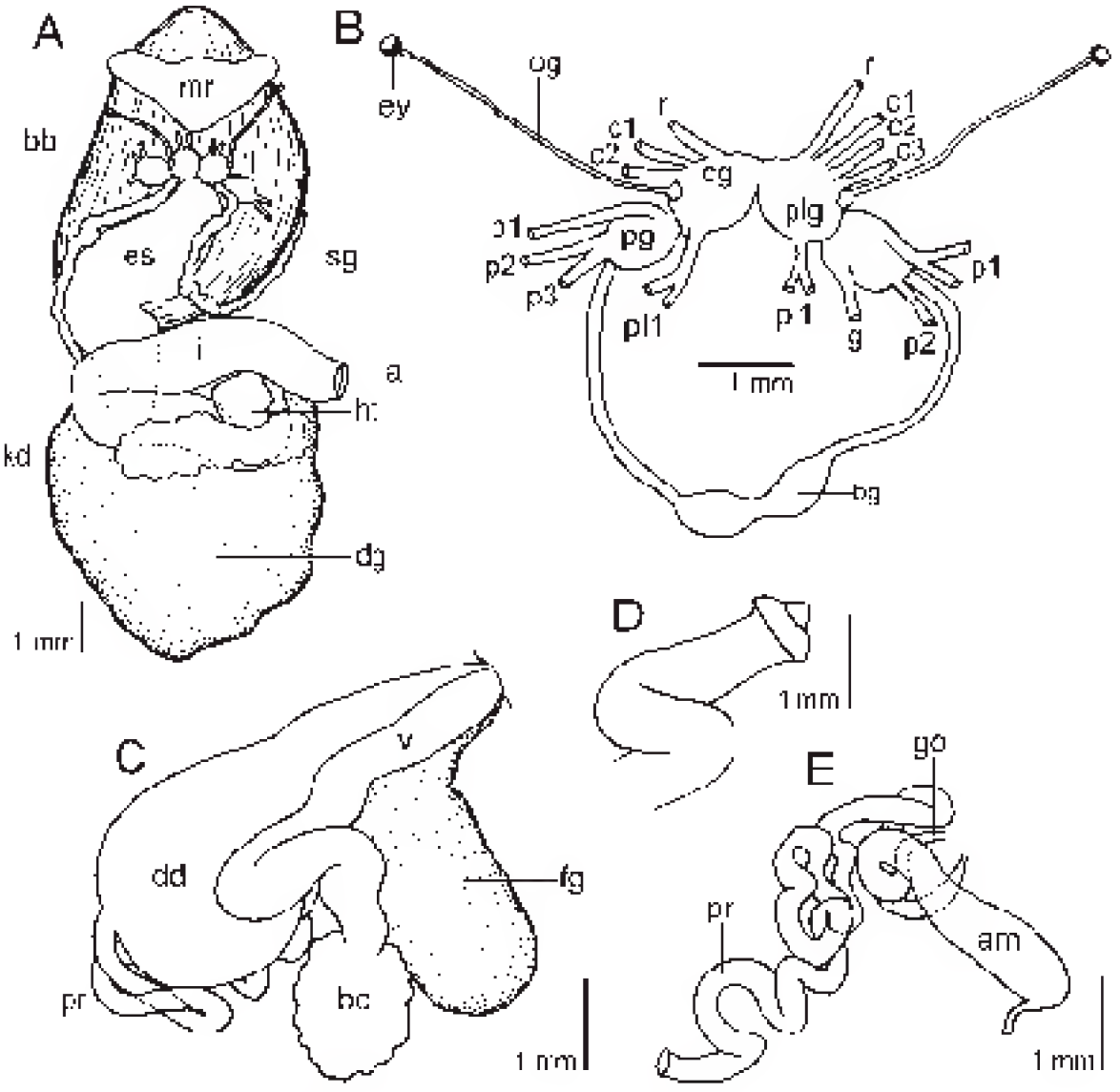

Figure 3. *Marionia tedi* Ev. Marcus, 1983, anatomy. A, Dorsal view of the general anatomy. B, Central nervous system. C, Reproductive system. D, Penis. E, Detail of prostate-ampulla connection. Abbreviations: a, anus; am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerve; cg, cerebral ganglion; dd, deferent duct; dg, digestive gland; es, esophagus; ey, eye; fg, female glands; g, genital nerve; go, gonoduct; ht, heart; i, intestine; kd, kidney; mr, muscular ring; op, optic ganglion; p, pedal nerve; pg, pedal ganglion; pl, pleural nerve, plg, pleural ganglion; pr, prostate; r, rhinophoral nerve; sg, salivary gland; v, vagina.

base of the rhinophores. There are no distinct gastro-esophageal nor rhinophoral ganglia. The pedal ganglia are clearly separated, having 3 nerves leading from the left one and 2 nerves from the right one. The genital nerve leads from the right pedal ganglion.

Circulatory and excretory systems. The circulatory system consists of a small heart situated on the central-right side of the body (Figure 3A). The excretory system has a large, glandular kidney (Figure 3A).

Biology

Specimens of *Marionia tedi* were collected or photographed on the gorgonian *Callogorgia americana* Cairns and Bayer, 2002, which most likely constitutes their prey. Examination of esophageal contents revealed the presence of an amorphous mass with no spicules or other recognizable structures.

DISCUSSION

The single specimen here examined fits within the variability of *Marionia tedi* Ev. Marcus, 1983, and there-

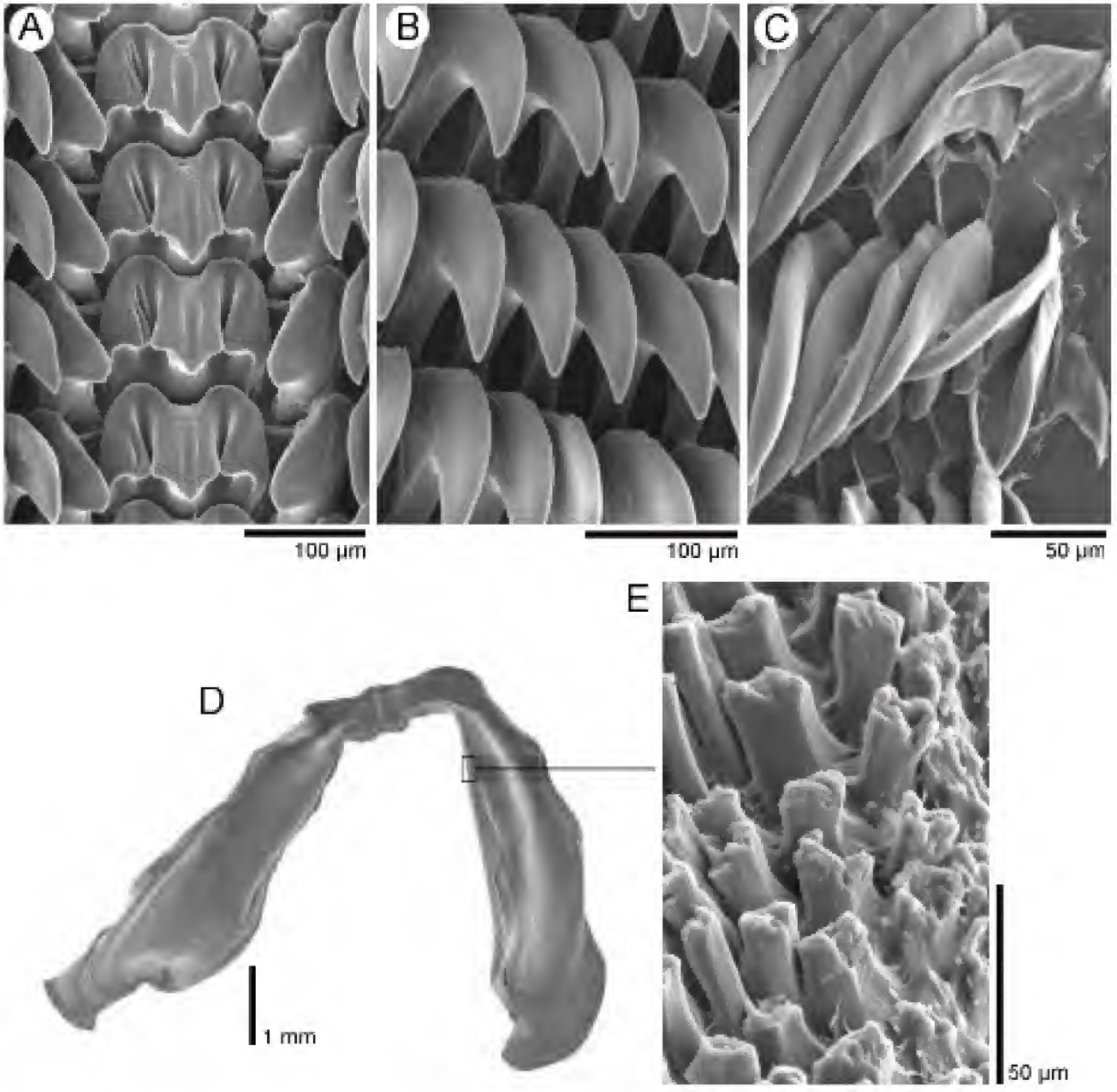

Figure 4. *Marionia tedi* Ev. Marcus, 1983, scanning electron micrographs of radula and jaws. A, Rachidian and innermost lateral teeth. B, Mid-lateral teeth. C, Outer lateral teeth. D, Jaws. E, Jaw masticatory border.

fore it is assigned to this species. *Marionia tedi* was originally described based on several specimens collected from the southern Gulf of Mexico, the Straits of Florida, and the southeastern Caribbean Sea at depths between 60–348 m. The specimen here examined is from nearly 300 m deeper than any of the others previously recorded. The internal anatomy of the species is very variable, particularly the morphology of the radula and jaws (see Marcus 1983). Very little is known about the environment on which the original specimens were collected, with the exception that they were dredged off hard or rocky bottoms. The radular morphology of the specimen here described is very similar to Ev. Marcus' specimen 64 from the Straits of Florida, showing shorter and wider lateral teeth compared to the other specimens. No other species of *Marionia* has been described from the western Atlantic.

This is the first species of opisthobranch mollusk recorded from a cold seep. A species of Dendronotidae, *Dendronotus comteti* Valdés and Bouchet, 1998, was described from the Lucky Strike hydrothermal vent in the Mid-Atlantic Ridge (Valdés and Bouchet 1998), constituting the only previous record of a shell-less gastropod from

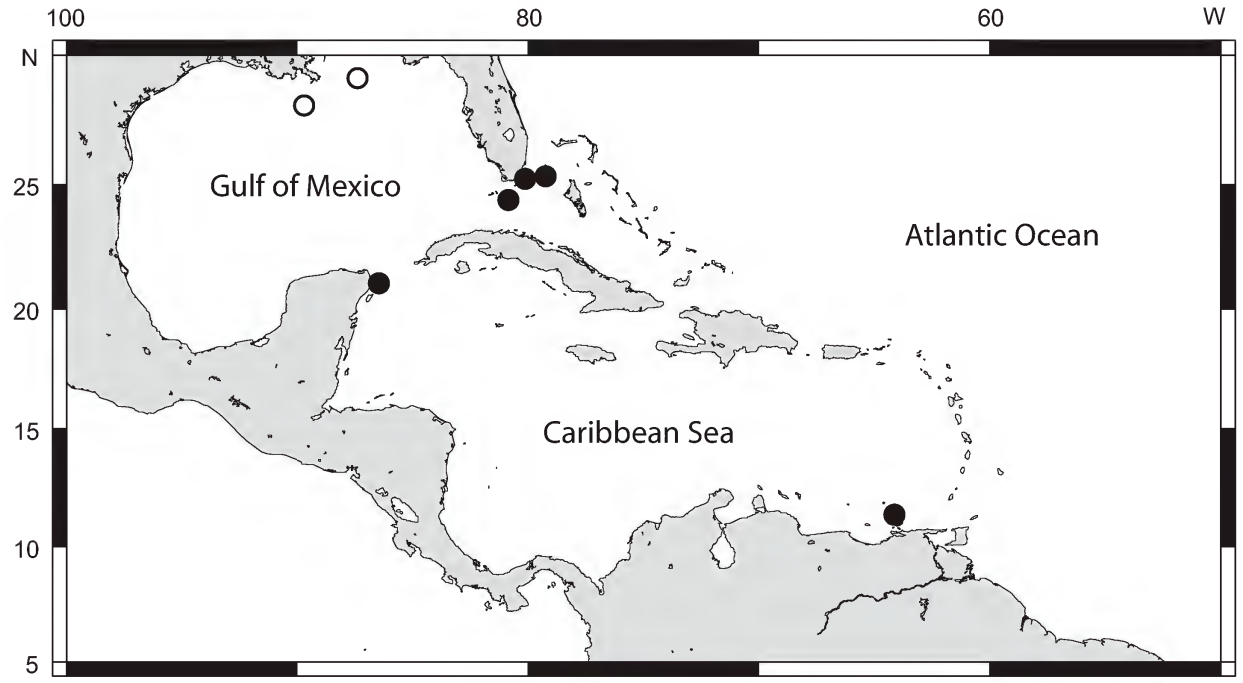

Figure 5. Map of collecting localities of specimens of *Marionia tedi* Ev. Marcus, 1983. Solid circles = historic collections; white circles = new collections.

deep-sea chemosynthetic-based environments. Valdés and Bouchet (1998) argued that the lower toxicity and unique chemical composition of the Lucky Strike hydrothermal field probably accounts for the presence of an uncovered nudibranch species. Additionally, *D. comteti* appears to inhabit the cooler peripheral areas of the vent, where high concentrations of its hydroid prey were also found.

Whereas *Dendronotus comteti* appears to be an endemic to hydrothermal vent environments, *Marionia tedi* is probably an opportunistic visitor. The latter was previously recorded from 5 other localities (Figure 5), none of which appear to correspond to known cold seep environments. Original specimens of *M. tedi* were collected during the R/V *John Elliott Pillsbury* and R/V *Gerda* expeditions in the tropical western Atlantic. There is not much environmental or ecological information available for those sites, but a review of faunal compositions cited in the report of the R/V *John Elliott Pillsbury* expedition (Voss 1967) and other monographs on mollusks collected by these 2 expeditions (Bayer 1971), contains no records of species indicative of cold seeps in the areas where specimens of *M. tedi* were collected.

Marionia tedi most likely feeds on *Callogorgia americana* Cairns and Bayer, 2002; the 2 nudibranch specimens observed alive were crawling on individuals of the gorgonian (Figure 1). Two subspecies of *C. americana* are currently recognized (Cairns and Bayer 2002), *C. americana americana* is widespread in the Caribbean: Straits of Florida, Campeche Bank, and Lesser Antilles from Puerto Rico to Venezuela. *Callogorgia americana delta* Cairns and Bayer, 2002 is endemic to the northern Gulf of Mexico: Green Canyon and Viosca Knoll; Cairns and Bayer (2002) do not describe the environments from which specimens of *C. americana delta* were collected, but the collecting localities are rich in cold seeps where this taxon has been recorded (Cordes 2004). Hydrocarbon cold seeps often produce carbonate substrates by authigenic precipitation, which generate hard bottoms for gorgonian settlement (Cordes 2004). The geographic range of both subspecies of *Callogorgia americana* perfectly matches the range of *Marionia tedi* (Figure 5) suggesting a close relationship between the 2 species.

Acknowledgements

I am very grateful to Janet Voight for making the specimen available for study and for providing all kinds of useful information regarding the collection site and cold seep environments. Erik Cordes provided me with photographs of the living animals and additional station data. Stephane Hourdez captured the photograph of one of the living animals. Finally, Nancy Voss provided me with a copy of the R/V John Elliott Pillsbury Expedition report and other useful bibliographic information.

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New Records for *Cubanocuma gutzui* Băcescu and Muradian, 1977 (Crustacea: Cumacea: Nannastacidae) from the Western Atlantic

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SHORT COMMUNICATION

NEW RECORDS FOR *CUBANOCUMA GUTZUI* BĂCESCU AND MURADIAN, 1977 (CRUSTACEA: CUMACEA: NANNASTACIDAE) FROM THE WESTERN ATLANTIC

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Introduction

The nannastacid cumacean genus *Cubanocuma* was erected by Băcescu and Muradian (1977) to accommodate a new, small species, *C. gutzui* Băcescu and Muradian, 1977, that was described from several specimens collected from six shallow water sites off the coast of Cuba. This little cumacean is distinctive and easily recognized by its a large and anteriorly truncated, nodulose carapace (Figure 1). The adult male holotype measured only 1.76 mm total length. The type locality is off Batabanó, Cuba (22°70'N, 81°80'W), 3 m depth, from "muddy sand with *Thalassia*" (Băcescu and Muradian 1977:8). In addition to the type locality, Băcescu and Muradian (1977:3) reported the species from "in front of Havana" and from Ana María Gulf, in depths ranging from 6 to 12.5 m. The substrata types from habitats where specimens were collected included "muddy sand with coral scraps," "rough sand with *Thalassia*," and "spongiae." Băcescu (1992), in the *Crustaceorum Catalogus*, maintained that the only record was that of the type. Apparently, Băcescu (1992) was unaware of a report for the genus from Bermuda by Markham and Sterrer (1986, in Sterrer 1986). Markham and Sterrer (1986:362) reproduced some of the original figures for *C. gutzui* from Băcescu and Muradian (1977) and also provided a brief rewritten synopsis of the diagnostic characters (1986:364). They believed their Bermuda specimens to be the same or a very similar species, referring to "*Cubanocuma* cf. *gutzui*," and reporting it as "not uncommon" on "silty bottoms in inland seawater caves" (Markham and Sterrer 1986). Later, Petrescu and Sterrer (2001) illustrated material also referred to "*Cubanocuma* cf. *gutzui*," which they considered synonymous with *Campylaspis cousteaui* Petrecsu, 1990, a species also described from Bermuda. They ambiguously listed *C. gutzui* Băcescu and Muradian, 1977, and *C. cousteaui* as synonyms under *C.* cf. *gutzui.* Iorgu Petrescu (Museum d'Histoire naturelle "Grigore Antipa," Romania) and W. Sterrer (Bermuda Aquarium Natural History Museum and Zoo, Bermuda) in personal communications with one of the authors (JWM) have confirmed that the Bermudan material did, in fact, represent true *Cubanocuma gutzui* Băcescu and Muradian, 1977 (=*Campylaspis cousteaui* Petrescu, 1990).

There are some additional published reports from Caribbean and Bahamian waters. In the Caribbean *C. gutzui* has been recorded as *Campylaspis cousteaui* Petrescu, 1990, from Jamaica (Petrescu et al. 1993) and Honduras (Petrescu 2003). In the Bahamas it was reported from Abaco, Andros, and Exuma (Petrescu 1996, 2003).

Because the original description and many subsequent records for *C. gutzui* have appeared in a Romanian journal, Travaux du Muséum d'Histoire naturelle "Grigore Antipa," which has limited distribution in the west, many workers studying tropical western Atlantic crustaceans still remain unaware of both the genus and species. Also, the species may have gone unrecognized (recorded as an odd specimen of *Campylaspis*, for instance) or may have been overlooked because of its small size. As part of an ongoing survey of the marine invertebrates of Guana Island, British Virgin Islands (BVI) (led by T.L. Zimmerman and J.W. Martin), numerous specimens of this nannastacid species were collected extending the known range eastward to the BVI. At the same time, the examination of other regional collections by two of us (RWH, TJH) established the presence of this species in Southeast Florida and the Gulf of Mexico (GOM), and we have found additional material from the southern Bahamian region and the northern Caribbean. In this note, we list the known occurrences of *Cubanocuma*, comment on the habitat, and mention certain morphological features observed from scanning electron microscopy (SEM).

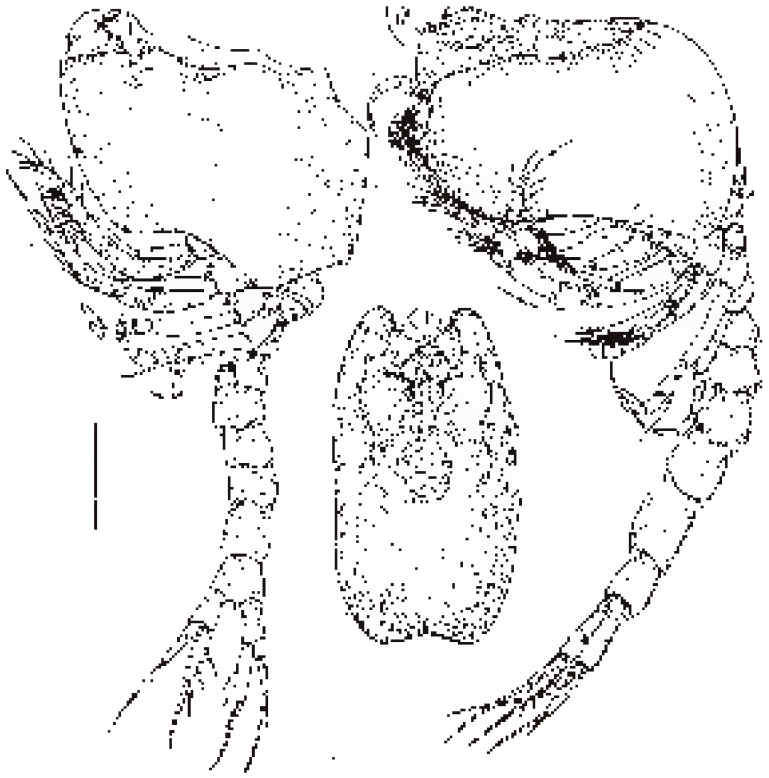

Figure 1. ***Cubanocuma gutzui*** **Băcescu and Muradian, 1977. From left to right. Female, lateral aspect; male, dorsal view of carapace; male, lateral aspect . Modified slightly from Băcescu and Muradian 1977:4 (Figure 1). Scale = 0.2 mm.**

MATERIALS AND METHODS

Most of the specimens from Florida and the GOM resulted from NOAA or EPA surveys, and vouchers and sorted material were often retained by these agencies. These records come from the personal laboratory notes of T. Hansknecht. Specimens from the BVI are housed at the Natural History Museum of Los Angeles County. Specimens from Bermuda are catalogued in the Bermuda Aquarium and Museum of Zoology. Specimens from South Florida, Florida Middle Ground, Turks and Caicos, and Grand Cayman are housed in the Gulf Coast Research Laboratory, Ocean Springs, MS.

RESULTS

Taxonomy

Order Cumacea Krøyer, 1846
Family Nannastacidae Bate, 1866
Genus *Cubanocuma* Băcescu and Muradian, 1977
Cubanocuma gutzui Băcescu and Muradian, 1977:3–9 (Figures 1–3)

Synomyms. *Cubanocuma gutzui*, 1977:3–9 (Figures 1–3); Ortiz and Lalana 1988:15; Petrescu and Sterrer 2001:195–196 (Figures 2–11); Petrescu 2003:121; 2004:90.—*Cubanocuma* cf. *gutzui*: Markham and Sterrer 1986:362 (Plate 120), 364; Petrescu and Sterrer 2001:95–96 (Figures 2–11).—*Campylaspis cousteaui* Petrescu, 1990:9–12 (Figure 1); Petrescu and Sterrer 2001:95–96 (Figure 2–11); Petrescu et al. 1994:392 (Figure 11)-393; Petrescu 1996:158, 160, 161 (Figure 2).

Diagnosis. (modified from Băcescu and Muradian 1977). Nannastacidae. Body small, compact, length 1.5–2.0 mm. Carapace relatively large, deep, covering part of free thoracic segments; eye lobe prominent, especially in male; fronto-pseudorostral line short, sinuous, nearly transverse. Antenna of male with peduncular article 5 slightly longer than article 4; flagellum short, not extending much beyond carapace, articles bearing numerous aesthetascs. Maxillipeds 1–3 similar to genus *Campylaspis*. Exopods present on thoracopods 3–6 (maxilliped 3, legs 1–3) of male and thoracopods 3–5 (maxilliped 3, legs 1–2) of female.

Remarks. Only one other Northwest Atlantic species, *Normjonesia danieli* Petrescu and Heard, 2002, presently known only from the mid-Continental Shelf (88 m) off southwestern Florida, appears superficially similar to *C. gutzui*. *Normjonesia danieli*, which like *C. gutzui* belongs to a monotypic genus, appears to be a deeper water

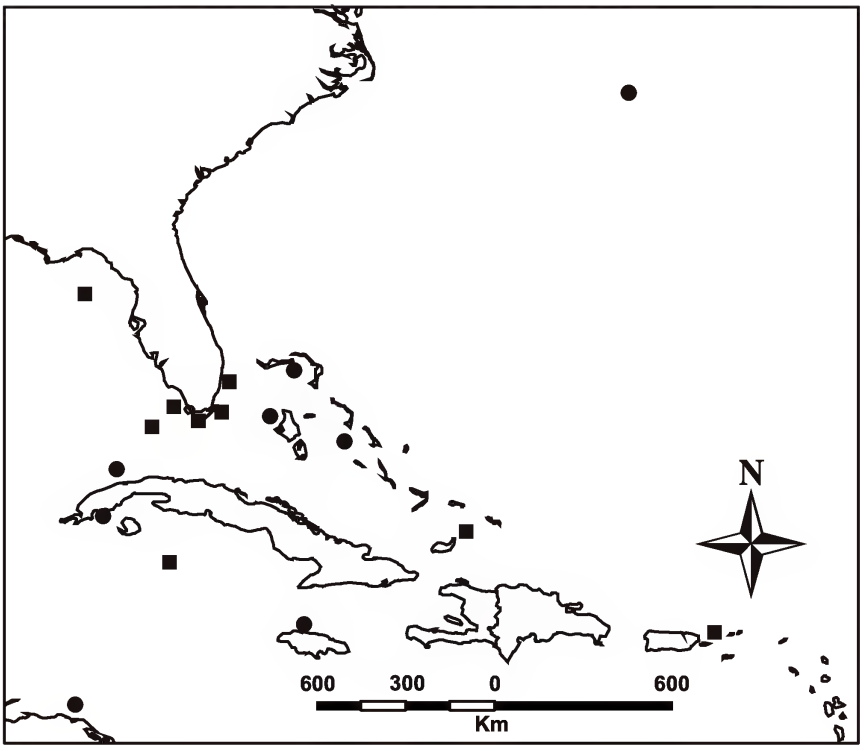

Figure 2. Map showing the general distribution of *Cubanocuma gutzui*. Black circles represent previously published records and squares indicate new distribution locations.

species. Morphologically it can be distinguished from *C. gutzui* by having 1) a more prominent, upturned pseudorostrum, 2) strong spines on the carapace, 3) exopods absent on the female, and 4) 5 pairs of exopods present on the male (Petrescu and Heard 2001).

New Records for *Cubanocuma gutzui* from the Northwest Atlantic (see Figure 2)

USA

Florida/ Port Everglades.—15 specimens from shallow reef, *Acropora cericornis* rubble, 26°09.63'N, 80°05.412'W, 6–7 m. Collection made as part of artificial substratum study conducted by Judy Roberts, Nova Institute of Marine Science.

Florida/Biscayne Bay. NOAA.—1 spec., Sta. 162, 25°79.30'N, 80°18.00'W, 4.6 m, 7 Jun 1996.—3 spec., Sta. 175, 25°78.60'N, 80°14.70'W, 4.0 m, 5 Jun 1996.—1 spec., Sta. 181, 25°71.10'N, 80°21.40'W, 2.7 m, 29 Jun 1996.—1 spec., Sta. 183, 25°69.70'N, 80°19.90'W, 3.5 m, 29 Jun 1996.—3 spec., Sta. 188, 25°60.60'N, 80°22.50'W, 2.7 m, 29 Jun 1996.—1 spec., Sta. 198, 25°61.20'N, 80°22.60'W, 2.4 m, 26 Jun 1996.—20 spec., Sta. 216, 25°40.40'N, 80°26.90'W, 1.5 m, 25 Jun 1996.—7 spec., Sta. 218, 25°34.20'N, 80°30.00'W, 2.4 m, 25 Jun 1996.

Florida Keys. EPA.—1 spec., Sta. KWS, 24°27.20'N, 81°52.70'W, 7 m, live bottom, 3 Nov 1994.—6 spec., Sta. KWR, 24°32.00'N, 81°49.45'W, 7–10 m, 80% sand substratum, 3 Nov 1994.—6 spec., Sta. KWT, 24°32.00'N, 81°48.80'W, 7–10 m 82%, sand substratum, 3 Nov 1994.

Florida Keys/Dry Tortugas. NOAA.—1 spec., Sta. 163, 24°42.260'N, 83°41.019'W, 63 m, shell/rock substratum, 4 Aug 1999.—1 spec., Sta. 134, 25°13.590'N, 81°56.246'W, 16 m, sand/shell substratum, 9 Aug 1999.

Florida/adjacent Southeast GOM. NOAA.—1 spec., Sta. MR04, 24°70.42'N, 81°57.15'W, 1.1 m, 8 Sep 1994.—1 spec., Sta. MR04, 24°70.45'N, 81°57.15'W, 1.5 m, 29 Aug 1996.—1 spec., Sta. MR36, 25°33.60'N, 81°34.63'W, 5.4 m, 1 Sep 1994.—1 spec., Sta. MR36, 25°33.76'N, 81°34.52'W, 6.0 m, 30 Aug 1995.—1 spec., Sta. MR37, 25°05.40'N, 81°57.10'W, 9.6 m, 8 Sep 94.—1 spec., Sta. WI96LR36, 24°91.45'N, 81°11.53'W, 4.1 m, 15 Aug 1996.—1 spec., Sta. WI96LR40, 24°87.40'N, 80°79.67'W, 2.5 m, 13 Aug 1996.—6 spec., Sta. WI96LR43, 24°85.14'N, 80°85.90'W, 2.1 m, 13 Aug 1996.—4 spec., Sta. WI97LR50, 23°77.10'N, 81°03.25'W, 2.0 m, 19 Aug 1997.—7 spec., Sta.WI97LR51, 24°76.22'N, 81°11.77'W, 2.4 m, 13 Aug 1997.

Florida Middle Ground (FMG). Northeast GOM, [28°–29°N, 84°–84°25'W]. Minerals Management Service sponsored study.—4 ♀♀, FMG III, Habitat 3.—2 ♂♂, 10

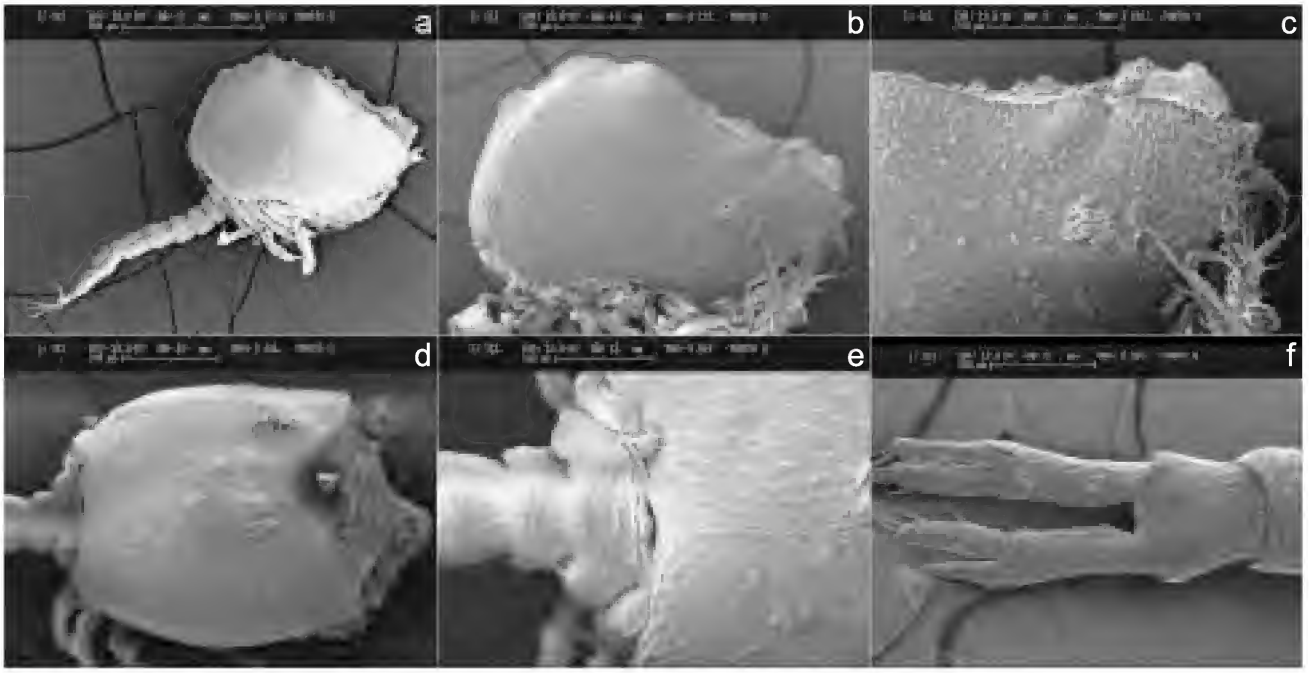

Figure 3. ***Cubanocuma gutzui*** **Băcescu and Muradian, 1977. SEM views of selected morphological features. Lateral aspect, a–c; a, entire specimen; b, enlargement of carapace; c, further enlargement of carapace showing anterior region (tuberculation of ocular and rostral areas). Dorsal aspect, d–f; d, view of entire carapace; e, enlargement of posterior part of carapace indicating presence of a mid-dorsal suture; f, last abdominal segment and uropods.**

♀♀, 7 juvs., FMG III, Habitat 5.—1 ♂, 2 ♀♀, FMG III, Habitat 7.—2 ♂♂, 7 ♀♀, FMG III, Habitat 9.—1 ♂, 7 ♀♀, 5 juvs., FMG III, Habitat 10.—1 ♂, 7 ♀♀, FMG 1V, Habitat 5.—21 spec., FMG III, Habitat 8.—10 specs., FMG III, Habitat 10.

The FMG collections were made during 1978 and 1979. Two other nannastacid cumaceans, *Cumella garrityi* Băcescu and Muradian, 1977 and *Campylaspis heardi* Muradian, 1880, co-occurred with *C. gutzui* in the diver-deployed and retrieved artificial habitats (see description in Modlin 1984) from the FMG.

Caribbean Sea

Guana Island, BVI. About 30 specimens from different shallow water (≤ 10 m) localities around this small island were collected. Most of the specimens examined for this report came from Station 12, Vc0944, of the Zimmerman and Martin survey, for which the collecting data are: Long Point, about 70 m southeast of dock (18°29.153'N, 64°34.971'W), above crest of reef, in more protected area in furrow on the bottom, covered with fine algae growing on small pebbles. Collected by T. Zimmerman and G. Hendler, 5 Jul 2000, depth about 3.5 to 4.5 m. The covering of algae was dominated by *Amphiroa fragilisima* with interwoven *Spyridia*, *Centroceras*, *Griffithsia lobifera*, and *Gelidium pusillum.*

Grand Cayman, Cayman Islands.—18 spec., 29 Aug 1996.—29 spec., 1 Sep 1996.—4 spec., between fringing reef and "The Edge" south shore, depth ~1 m, carbonate rock washings 23 May 1998 (see map in Price et al. 2002).

Pine Cay, Turks and Caicos.—3 females, Rack Cay, Caicos Banks about 1 km east of Pine Cay (refer to map in Schotte et al. 1991), rock washings, ~1 m depth, 12 Apr 1988.

COMMENTS

Morphology

Female specimens from Guana Island were examined using SEM (Figure 3) and agreed strongly with the original description (Băcescu and Muradian 1977). With the use of SEM, we confirmed many of the fine details mentioned in their text and illustrations, including such features as the minute sculpturing and scales on the carapace and appendages. One feature not depicted or mentioned in their account is the fine suture line extending along the dorsal midline of the carapace (Figure 3).

Habitat and Distribution

Based on the information collected during this study, the genus *Cubanocuma* is widely distributed in the shallow

waters of the American Mediterranean, i.e., Bermuda, Bahamas, South Florida, GOM, and northeastern and northwestern Caribbean. Based on the above observations, and assuming that all known records of the genus are of the same species (*C. gutzui*), the microhabitat varies widely as well. Although the species was originally reported from Cuba from muddy sand, Markham and Sterrer (1986) reported it from "silty bottoms in inland seawater caves" where they stated that it was "not uncommon." One of us (RWH) recently (Aug 2004) collected specimens from rock washings at a depth of about 1 m at the opening of Harrington Sound, Bermuda. This species has been found associated with algal mats and sponges on Grand Cayman and Pine Cay (R. Heard, pers. obser.). Most of the specimens from Guana Island came from a relatively protected area containing gravel covered by a layer of fine algae. Thus, it appears that *C. gutzui* thrives in a variety of shallow, warm water habitats, and therefore one might expect to encounter this species on or adjacent to shallow, live bottom habitats having carbonate sediments in many areas within the American Mediterranean.

ACKNOWLEDGMENTS

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